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EVOLUTION OF AQUATIC HABITATS WITH SPECIAL REFERENCE TO THE DISTRIBUTION OF CORIXIDAE

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(*With Plate* 1 *and* 2 *Figures in the Text*)

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1. INTRODUCTION

CORIXIDAE, sometimes known as "lesser water-boatmen", are an aberrant family of the Hemiptera Heteroptera (Fig. 1). They are found in most stagnant or nearly stagnant aquatic habitats where the depth of water does not exceed about one metre, and where there is a bottom of relatively fine soil particles. There are some 30 species in the British List, many of them being common and widely distributed; moreover, nearly all, where they do occur, are found in large numbers. The group is, therefore, particularly suitable for the study of problems of distribution and the relation between a species and its environment. Before any attempt is made to explain it, the distribution of a group must be described.

It is the purpose of the present paper to describe the distribution of the species of Corixidae found in an area in the central and southern parts of the Lake District, a mountainous region with peaks rising up to 970 m. (3000 ft.) in the north-west of England. Fig. 2 shows the topography of the area and the position of the water bodies studied. Each one has been plotted on 6 in. to the mile maps, and these maps with ecological data and a collection of over 5000 specimens are now lodged in the laboratory of the Freshwater Biological Association.

The following species of Corixidae were recorded from the area:

Sigara sahlbergi (Fieb.)	*S. scotti* (Fieb.)	*Corixa geoffroyi* Leach
S. linnei (Fieb.)	*S. nigrolineata* (Fieb.)	*C. dentipes* (Thoms.)
S. castanea (Thoms.)	*S. praeusta* (Fieb.)	*Sigara hieroglyphica* (Duf.)
S. striata (Linn.)	*S. wollastoni* (D. & S.)	*S. limitata* (Fieb.)
S. falleni (Fieb.)	*S. carinata* (Sahlb.)	*S. semistriata* (Fieb.)
S. distincta (Fieb.)	*Cymatia bonsdorffi* (Sahlb.)	*S. concinna* (Fieb.)
S. venusta (D. & S.)	*Micronecta poweri* (D. & S.)	*S. germari* (Fieb.)
S. fossarum (Leach)		

All the species in the two left-hand columns were found dominant in one or more localities; those in the right-hand column were never dominant.

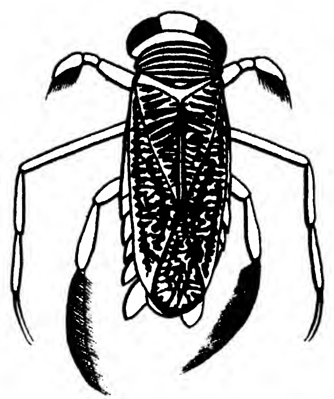

Fig. 1. Sigara scotti (× 75)

On the advice of Mr W. E. China of the British Museum of Natural History, to whom my thanks are due, I have adopted the names used in the most recent comprehensive work on the Corixidae of West Europe (Poisson, 1935). The names referred to the genus *Sigara* in the above list will be more familiar under the name "*Corixa*", and the genus *Micronecta* will be more familiar under the name "*Sigara*".

I am indebted to Mr G. A. Walton of Bristol University for the identification of *Micronecta poweri*. In two papers on the fauna of Windermere this species has been referred to as *Sigara minutissima* (Moon, 1934, 1936.)

2. Methods

The collections were made with a hand-net since in many localities the bugs were so sparse that a quantitative grab would not have secured a significant number. Where there was more than one type of littoral plant community in a single body of water, a station was worked in each. At all stations an attempt

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Key to Fig. 2.

1. Brown Cove Tarn	20. Slew Tarn	39. Wise Een Tarn
2. Red Tarn	21. Loughrigg 10	40. Wise Een Fishpond
3. Knott's Dock Tarn	22. Low Water	41. Three Dubs Tarn
4. Blea Tarn (Wythburn)	23. Tarn Hows	42. Moss Eccles Tarn
5. Harrop Tarn	24. Rose Castle Tarn	43. School Knotts Tarn
6. Grisedale Tarn	25. Arnside Tarn	44. Cleabarrow Tarn
7. Brother's Water	26. Stephen How	45. Crook Reservoirs
8. Styhead Tarn	27. Barngates Quarry	46. Rather Heath Tarns
9. Sprinkling Tarn	28. Lost Tarn	47. Lindeth Tarn
10. Stickle Tarn	29. Blelham Fishpond	48. New Tarn
11. Codale Tarn	30. Blelham	49. Knipe Tarn
12. Easedale Tarn	31. Clay Pond	50. Gill Head Fishpond
13. Blindtarn Moss	32. Monk Coniston 1	51. Gill Head Reservoir
14. Whitemoss Reservoir	33. High Man Tarn	52. Podnet Tarn
15. Blea Tarn (Langdale)	34. Goosefoot Tarn	53. Little Ludderburn Tarn
16. Lingmoor Tarn	35. Wray Mires Fishponds	54. Kirby Quarries
17. Little Langdale	36. Hodson's Tarn	55. Knittleton Lake
18. Elterwater	37. Robinson's Tarn	56. Great Green Hows Reservoir
19. Loughrigg	38. Wray Mires Tarn	57. Helton Lake

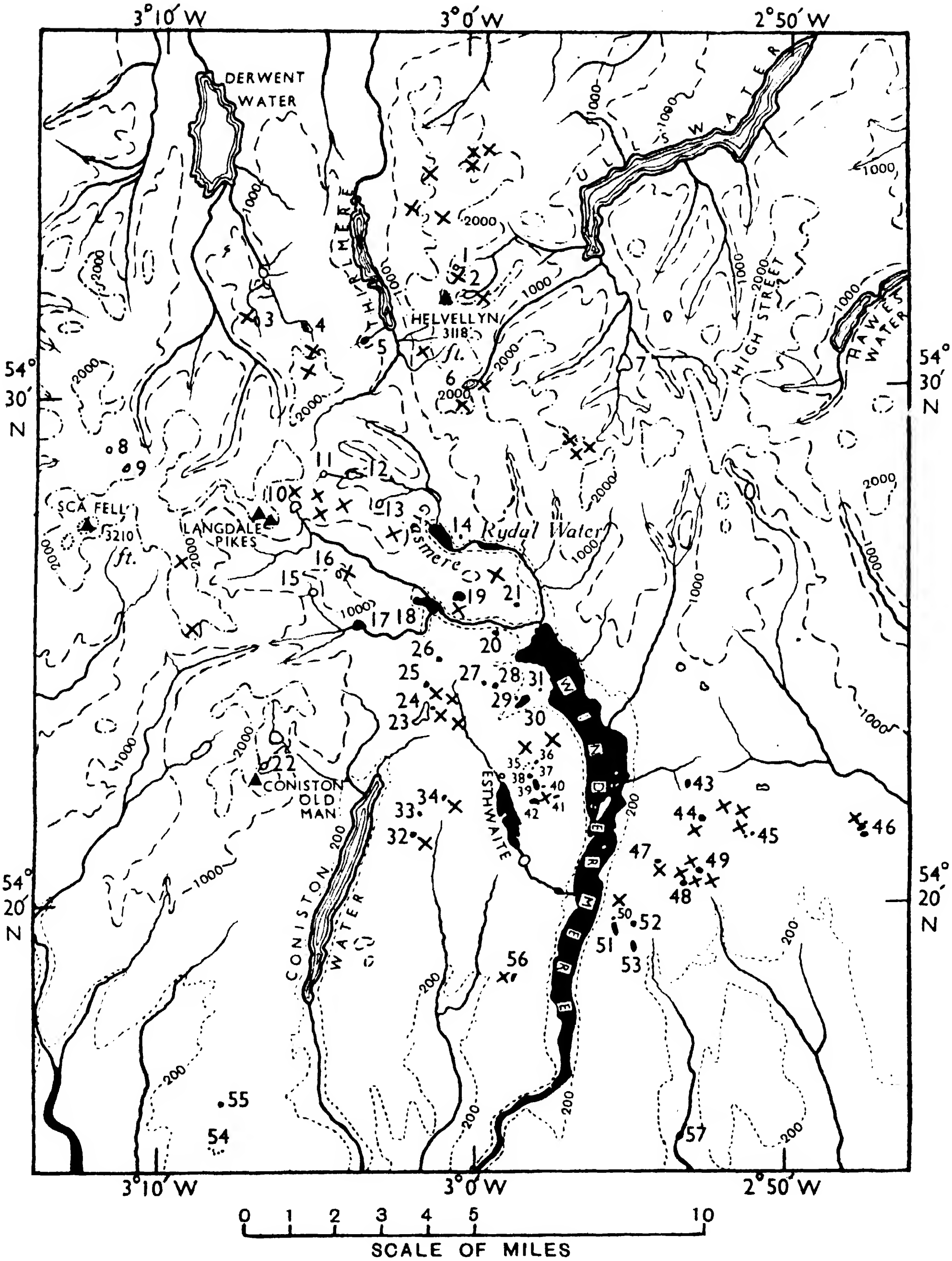

Fig. 2. Sketch-map of the Central and Southern portions of the Lake District. Contours 200, 1000, 2000 and 3000 ft. Lakes and tarns from which Corixidae were recorded are shown in black; lakes and tarns where no Corixidae were found or where no collecting has been done are shown in outline. The position of pools is indicated by a cross.

For key see opposite page.

was made to collect 20 to 30 Corixids within the smallest possible area. Since it is unlikely that one species can escape a pond net more readily than another, figures for each species in one catch are strictly comparable, but the total numbers for each catch give little idea of the abundance of the bugs at the station where the catch was made.

In order to obtain a physical estimate of the nature of the soil underlying the water, the percentage of organic matter in the soil (subsequently referred to as % o.m.s.) was measured by the ignition of a dried sample. This method is reliable, as calcium carbonate is present in negligible amounts; but the figures must be treated as approximate, since it was not possible to examine sufficient samples to eliminate local variations in the % o.m.s. in each locality, and a further error was introduced by the difficulty of freeing the samples from living roots. The nitrogen content of some soil samples was determined by Kjeldahl's method. In calculating the carbon/nitrogen ratio the carbon content of the soil is taken to be half the organic matter. The *p*H value of the water was taken in the field by means of indicators and comparison with standard buffer solutions. The colour of the water was measured by the methyl orange method of Ohle (1934).

3. Aquatic habitats in the area

Conditions are singularly uniform throughout the area. The rocks, Borrowdale volcanic series and Bannisdale slates, are hard, the vegetation is chiefly rough grassland or moorland, and the waters are poor in salts, particularly those of calcium. The bodies of water fall conveniently into three classes: (*a*) pools, (*b*) tarns, (*c*) lakes.

Pools are shallow collections of water lying in rock crevices or in hollows in thick layers of peat; while tarns and lakes are collections of water lying in eroded rock basins and/or held up by dams which may be of glacial or artificial origin. The distinction between tarns and lakes is not clear cut, but in general tarns are smaller and shallower, fed by smaller streams, and situated on the top or side of a hill, while lakes are larger and deeper, fed by rivers and situated in the main valleys. In the area studied the surface area of the tarns ranges between 500 and 200,000 sq. m. and the depth probably seldom exceeds 10 m. The surface area of lakes ranges between 90,000 and about 15,000,000 sq. m. and the deepest (Windermere) has a maximum depth of 67 m.

This classification on physiographic features has the merit of convenience and simplicity, but before studying these three classes of water body as environments inhabited by animals and plants it is desirable to look for some more fundamental distinction between them.

It has been shown by Pearsall (1920, 1921) that one such distinction is the *proportion of bases present in the water*, a factor dependent on the rate at which *silting* is taking place. This affects all aspects of lake biology, but for the

Phot. 1. Grisedale Tarn. A barren natural tarn. *Corixa wollastoni* occurs in the small pool near the end of the tarn.

Phot. 2. Stephen How. Habitat of *Sigara scotti*.

present purpose it is necessary to consider only the relation between silt and the subaquatic soils.

Every aquatic habitat is continually evolving, a process which, in general, means that soil is accumulating and that the locality is, therefore, gradually filling up. This accumulating soil is made up partly of vegetable remains and partly of inorganic silt. Vegetable remains contribute organic matter and silt brings with it bases which enable this organic matter to be decomposed. Accordingly the amount of silt relative to the amount of vegetable remains determines the rate at which the percentage of organic matter in the soil (% o.m.s.) increases. The soil is first colonized by submerged plants, but with the increase in the % o.m.s. these submerged plants are replaced by species with floating leaves, which in their turn give place to others with an emergent habit. It is found that the component species in such a succession vary in different places, and that the factors determining what species shall make up the succession in any one place are related to the rate at which the % o.m.s. is increasing.

In the waters of the Lake District plant successions culminate in five different species of emergent. *Typha latifolia* grows on soils where the rate of increase of % o.m.s. is low, *Phragmites communis* where it is more rapid; while still higher rates of increase result successively in the appearance of *Scirpus lacustris*, *Equisetum limosum* and *Carex inflata*. Since most bodies of freshwater ultimately become dry land it is possible to go a stage further. Soils where the rate of increase of the % o.m.s. is low ultimately support woodland, those where it is high, moorland.

Thus study of the vegetation shows that a subaquatic soil varies in two important factors: on the one hand the *quantity* of organic matter present, on the other the *quality*, this latter depending on the rate at which the percentage of organic matter has increased. During the present investigation the actual percentage of organic matter present in the soil has been measured directly and its quality has been assessed from the species of plant found. The classification of water bodies may now be reconsidered from the point of view of the % o.m.s. and the rate at which it is increasing.

In *pools* there is little or no silting and therefore little decomposition of plant remains. There is a rapid increase in the % o.m.s. and a high figure is soon reached and thereafter maintained. Where there is a highly organic soil from the beginning (peat pools) the high value is merely maintained. *Tarns* receive some silt, but since their feeding streams are seldom of any size, only small quantities are brought in, and they too have a high % o.m.s. They become overgrown with *Carex* (e.g. Robinson Tarn) and finally give rise to moorland (e.g. Blindtarn Moss). In *lakes*, on the other hand, gradual weathering of the drainage area yields an abundant supply of silt and the % o.m.s. tends to remain low. The characteristic emergent plant is *Phragmites*. The ultimate end of a lake is probably moorland too (Rankin, 1911) for the growth

of large beds of *Phragmites* checks the flow of water, silt is available in decreasing quantity, the % o.m.s. increases rapidly and except in the neighbourhood of the stream channels (e.g. Rusland Moss) *Carex* becomes the dominant plant. However, it is convenient to distinguish tarns and lakes in the Lake District as bodies of water where, except in the extreme stages, *Carex* and *Phragmites* respectively are the dominant emergent plants.

Independent of the rate at which the % o.m.s. is increasing, the rate at which soil accumulates in any body of water will vary from place to place and so different places will be at different stages of evolution. The stage of evolution may be roughly gauged from an inspection of the surroundings and it is also indicated by the nature of the vegetation, whether submerged, floating leaved or emergent. From collections made at stations in different stages of evolution it is, therefore, possible to work out successions of animal species.

4. Distribution of Corixidae

(*a*) *General account*

There is evidence that the percentage of organic matter in a soil is also an important factor in the distribution of certain species of Corixidae. Further there is, as in plants, a succession of species as the % o.m.s. increases, and the species making up a succession are different at different rates of increase. Since the rate of increase of the % o.m.s. can only be roughly gauged by the species of plant growing, and since the superficial layers of soil on which the Corixids are found are those most liable to local variation in the % o.m.s., an exact correlation between the % o.m.s. and the species of Corixid is not to be expected. Nevertheless, the results suggest that there is a definite correlation between the two. At present the evidence is based entirely on field observations, and no attempt has been made to determine the nature of the relation between the type of soil and the species of Corixids living on it.

Most of the evidence obtained during the present investigation relates to the succession of species under conditions where the rate of increase of the % o.m.s. is rapid. It is taken from collections made in a number of reed-beds in Windermere and in many tarns and pools. Although Windermere is a relatively advanced lake and therefore receives much silt, most of the reed-beds are situated in bays which are fed by quite small streams. As a result, development of the bed tends to produce increasingly stagnant conditions within itself, the silt supply is reduced, and the % o.m.s. increases rapidly, ultimately producing a soil of high organic content resembling that found in tarns. Similarly, conditions over the greater part of many tarns approach those found in pools, and therefore these three types of water body represent successive stages of evolution under conditions where the rate of increase of the % o.m.s. is rapid.

Different reed-beds in Windermere are at different stages of evolution. Primitive beds, that is those with a low % o.m.s., are inhabited by *Sigara striata* and *Micronecta poweri*, a species which is found on all exposed shores, though most abundant on sand. In more advanced beds with a higher % o.m.s., *M. poweri* is not found, and *Sigara striata* is joined by *S. distincta* and *S. fossarum*, two species which in beds of yet higher organic content tend to replace *S. striata*. In beds with the highest % o.m.s., *S. scotti* is the dominant species.

S. distincta and *S. fossarum* are found in a certain number of tarns but only at stations where the % o.m.s. is relatively low. At other stations where it is higher they are replaced by *S. scotti*. Where emergent vegetation, clearly the last stage in the evolution of a body of water, provides thick cover *S. castanea* is the only species found. In pools *S. scotti* occurs where vegetation is sparse or absent; *S. castanea* where vegetation is thick.

Under conditions where the rate of increase of % o.m.s. is rapid there is, therefore, the following succession of Corixid species:

$$\textit{Micronecta poweri} \rightarrow \textit{Sigara striata} \rightarrow \left\{\begin{matrix} \textit{S. distincta} \\ \textit{S. fossarum} \end{matrix}\right\} \rightarrow \textit{S. scotti} \rightarrow \textit{S. castanea}.$$

There is unfortunately much less evidence about the succession of species under conditions where the rate of increase in the % o.m.s. is low. In this area such conditions are only maintained in reed-beds situated right at the mouth of a large stream. It seems probable, however, that *S. linnei* dominates such reed-beds and that at a later stage of evolution when willows have appeared and water is confined to marshy pools *S. sahlbergi* is the characteristic species. It appears to be associated with the presence of dead leaves under stagnant conditions. Although the evidence about this succession in the Lake District is very meagre, it is confirmed by collections made in the Little Sea, Studland (Diver and others), and it is noteworthy that Hutchinson (1926) collecting in Wicken Fen, a region where bases are abundant, records *S. striata* and *S. fossarum* from the lodes and more open stations, and *S. linnei* and *S. sahlbergi* from the *Phragmites* beds.

In eleven tarns there is a succession:

$$\textit{Sigara scotti} \rightarrow \textit{Cymatia bonsdorffi} \rightarrow \textit{S. linnei}$$

and with it is associated a fourth species, *S. praeusta*, whose relation to the others is still obscure. The only apparent difference between these tarns and the rest is that they all receive organic matter from some external source, either from dead leaves or animal fouling.

As pointed out above, pools are inhabited by *S. scotti* and *S. castanea*, but this only refers to those pools which lie below an altitude of approximately 450 m. (1500 ft.). Above this altitude *S. wollastoni*, *S. nigrolineata*, and occasionally *S. carinata* are the dominant species.

The evidence on which these conclusions are based may now be considered more fully, records for each of the three classes of water body being treated separately.

(b) *Detailed account*

(1) *Lakes.*

Most of the work has been done in the north basin of Windermere; but collections have also been made from other bodies of water which, although commonly called tarns, must (since the characteristic emergent plant is *Phragmites*) be considered lakes in the light of the definition already given (p. 6). In parts of Windermere sheer rock-faces may still be found, but along most of the shoreline they are either weathered to give the stony "Bannisdale shore" or are covered by glacial drift. Where headlands afford protection from wave action finer deposits cover the bottom, and here are found beds of vegetation comprising either plants confined elsewhere to deeper water (e.g. *Myriophyllum*, etc.), or plants with an emergent habit. In Table 1 these beds are arranged in order of the % o.m.s. It will be seen that *Phragmites* is the only plant in beds where the % o.m.s. is low, and that, as the percentage increases, *Scirpus* and *Carex* appear as well, indicating conditions of rapid increase.

Micronecta only occurs in beds where the % o.m.s. is very low. Its distribution is considered in detail later. The species of *Sigara* are only found under the sheltered conditions of the reed-beds, and it will be seen from the table that with the increase in the % o.m.s. there is a change in the composition of the Corixid population. *S. striata* is the only species in the beds where the % o.m.s. is low; in beds where the % o.m.s. is higher it is joined and finally to some extent replaced by *S. distincta* and *S. fossarum*, while in the beds, where the % o.m.s. is highest *S. scotti* is the dominant species. A similar relationship between the species is found in the other lakes studied (see Table 2).

Evidence about the succession under conditions where the rate of increase of the % o.m.s. is low is only forthcoming from two small lakes, both with a complete ring of *Phragmites* round the shores, and from two localities in large lakes. Helton Lake is fed by a river, and there is clearly an abundant supply of silt. Knittleton Lake is fed by a small stream but, although the development of reed-beds is extensive, *Phragmites* has not been replaced, and this indicates a low rate of increase of the % o.m.s. The dominant species in both lakes is *Sigara linnei*.

Where the rate of increase of the % o.m.s. is low a reed-bed is succeeded by a *Salix-Phragmites* swamp. Such swamps are found on the deltas of the main inflow of Esthwaite and the Blelham Beck, one of the larger feeders of Windermere. Water persists in a few places on these deltas and the only species of Corixid found is *Sigara sahlbergi*.

The distribution of *Micronecta poweri* may be considered in more detail. The records, summarized in Table 3, are largely taken from the data which Mr

Table 1

Locality	Vegetation	Nature of bottom	% o.m.s.	Date	*M. poweri*	*S. striata*	*S. distincta*	*S. fossarum*	*S. scotti*	*S. falleni*	*S. sahlbergi*
Brathay Bar	*Phragmites*	Gravel	—	17 Aug. 1936	—	**15**	—	—	—	—	—
Brathay Bay N.	,,	Sand	3·0	7 June 1936	**50**	**11**	—	—	—	—	—
Whitecross Bay E.	,,	,,	4·0	6 July 1936	**100**	**28**	—	—	—	—	—
Brathay Mouth E.	,,	,,	5·5	12 Mar. 1937	—	**19**	2	—	—	—	—
Sandy Wyke N.	,,	,,	6·5	7 June 1936	**35**	**17**	1	—	—	—	—
Sea Mew Bay	*Littorella*	,,	6·5	10 Aug. 1936	**35**	3	—	—	—	—	—
Littorella sward M.	*Phragmites*	,,	6·5	6 Dec. 1936	—	**17**	—	—	—	—	—
Littorella sward S.	*Myriophyllum*	Washed drift	6·5	6 Dec. 1936	—	**42**	—	—	—	—	—
Pull Wyke Stream	*Phragmites, Equisetum*	Sand	9·3	1 June 1936	—	**11**	—	—	—	3	—
Ecclerigg Bay	*Myriophyllum*	,,	10·0	4 Dec. 1936	—	**18**	—	—	—	—	—
Gale Naze W.	*Phragmites, Scirpus*	,,	11·5	15 Oct. 1936	—	**17**	4	2	—	—	—
Whitecross Bay W.	*Phragmites*	Clay	15·0	6 Dec. 1936	—	**70**	**25**	2	—	—	—
Waterhead E.	*Scirpus, Juncus*	Sand	15·5	12 Mar. 1937	—	**20**	**40**	—	—	—	—
Whitecross Creek	*Carex*	Mud	19·0	6 Dec. 1936	—	**24**	3	**10**	—	—	8
Fisherty Bay	*Myriophyllum*	Debris	22·0	21 Apr. 1936	—	**15**	**17**	—	—	—	—
Bee Bay a.	*Phragmites, Carex*	Clay	22·4	2 Dec. 1936	—	4	1	**18**	—	3	—
Congo Mouth W.	*Phragmites, Scirpus, Carex*	Fibrous	22·5	21 Feb. 1937	—	**23**	**29**	**12**	—	4	—
Congo	*Callitriche*	Mud	30·0	4 Oct. 1935	—	**28**	**13**	**10**	—	—	—
Brathay Bay W.	*Scirpus*	Sand	31·0	15 Oct. 1937	—	**30**	5	—	—	—	—
Pull Wyke BH.	*Phragmites, Carex*	Fibrous	32·5	24 Nov. 1936	—	3	**13**	8	—	—	—
Congo Mouth E.	*Scirpus*	Debris	35·5	4 Apr. 1937	—	**12**	**27**	3	—	2	—
Pull Wyke Swan	*Phragmites, Equisetum, Carex*	Mud	43·0	21 Feb. 1937	—	8	6	**18**	—	**12**	—
Congo Mouth N.	*Phragmites, Scirpus, Equisetum, Carex*	Fibrous	44·5	24 Nov. 1936	—	1	**16**	**15**	—	—	—
Union Bay	*Phragmites, Carex, Menyanthes*	Sand and debris	49·0	25 Oct. 1936	—	**9**	**9**	—	**18**	—	—
Bee Bay c.	*Phragmites, Scirpus*	Fibrous	51·0	2 Dec. 1936	—	**7**	**9**	**10**	—	1	—
Gale Naze E.	*Phragmites, Equisetum, Carex*	Mud	52·0	20 Aug. 1936	—	**32**	3	—	**35**	—	—

Figures in heavy type in Tables 1, 2, 5 and 6 are the dominant and subdominant species. In all except a few border-line cases, the rule has been to count those where the number (*a*) exceeded 10 and (*b*) exceeded 33 % of the number of the most abundant species.

Table 2

Note. Habitat subdivisions (*a*) etc. refer to field survey data on specimen labels.

Locality	Vegetation	Date	*S. striata*	*S. distincta*	*S. fossarum*	*S. scotti*	*C. bonsdorffi*	*S. venusta*	*S. falleni*
Little Langdale	*Scirpus*	25 Feb. 1936	**14**	—	—	—	—	—	—
Elterwater	(*a*) *Phragmites, Equisetum*	26 Feb. 1936	**42**	—	—	—	—	—	—
	(*b*) *Scirpus*	26 Feb. 1936	**26**	5	**10**	—	—	3	—
Grasmere	*Phragmites, Scirpus, Equisetum, Carex*	6 Mar. 1936	**11**	**14**	5	—	4	—	—
Rydal	*Phragmites, Equisetum, Carex*	5 June 1936	1	—	3	—	1	—	—
Esthwaite	(*a*) *Phragmites*	12 Mar. 1936	6	—	1	—	—	—	1
	(*b*) *Phragmites, Carex*	12 Mar. 1936	5	—	—	**17**	—	—	1
Blelham	*Phragmites, Carex*	18 Mar. 1936	**10**	—	**16**	—	—	—	—
Loughrigg	*Phragmites, Carex*	16 Oct. 1935	7	—	5	—	—	—	—

Table 3

Locality	Nature of substratum	Number of hauls	Number of hauls in which *Micronecta* found	Greatest number of *Micronecta* in one haul	Average number of *Micronecta* per haul
Bays 1 to 4	Exposed Bannisdale shore	21	4	2	1·25
South of Boathouse 3	Sheltered Bannisdale shore. Small tufts of *Myriophyllum* and filamentous green algae	9	7	30	12
Boundary Crag to Epley Head	Exposed drift shore	14	2	5	3
High Wray Bay	Sandy shore. Sparse *Littorella*	12	6	6	3
Sandy Wyke	Stony shores with sand and silt	119	56	27	2·3
	Sandy shore. Sparse *Littorella*	19	5	—	1·5
	Phragmites bed	15	3	1	1
	Scirpus bed	15	3	11	6
	Littorella sward, 3 ft.	2	0	—	—
	Littorella sward, 4 ft.	4	4	1	1
	Littorella sward, 5 ft.	3	3	1	1

H. P. Moon, who has made detailed surveys of the exposed shores of Windermere, has kindly put at my disposal. The hauls covered, where possible, an area of 1 sq. ft. (0·09 sq. m.) The survey of the exposed shore was carried out during July and August, the months when *Micronecta* is most abundant; the survey of the silted shore (Pull Wyke) extended over a whole year. *Micronecta* occurred down to a depth of 5 ft. (1·5 m.) but was most numerous between 0 and 2 ft. (0·6 m.). Subsequent collections by the writer with a hand net over the drift shore between Boundary Crag and Epley Head showed that *Micronecta* occurred in moss (*Fontinalis*) growing on stones close to the water's

edge and in a small patch of *Juncus articulatus*, but not elsewhere. The occurrence of *Micronecta* in the *Scirpus* bed does not agree with observations from other reed-beds (see Table 1). It appears from Mr Moon's notes, however, that it only occurred on sandy patches.

The following collections were made with a hand grab covering an area of 1 sq. ft. (0·09 sq. m.).

Table 4

Locality	Vegetation	Date	Bottom	Depth in.	Number of *Micronecta*
"Littorella sward"	*Littorella*	12 Aug. 1936	Sand	5	74
"Littorella sward"	*Littorella*	12 Aug. 1936	Sand	5	20
Brathay Bay N.	*Phragmites*	20 Aug. 1936	Sand	15	11
Brathay Bay N.	*Phragmites*	20 Aug. 1936	Sand and dead leaves	9	0
Fisherty Bay	*Littorella*	21 Aug. 1936	Sand and gravel	26	4
Fisherty Bay	*Myriophyllum*	21 Aug. 1936	Sand	17	0
Fisherty Bay	*Potamogeton natans*	24 Aug. 1936	Vegetable debris	18	0
Fisherty Bay	*Littorella*	24 Aug. 1936	Gravel	6	3

The "*Littorella* sward" is an extensive area of sand and gravel. *Littorella* is abundant and grows right up to the water's edge, and small patches of *Myriophyllum* and filamentous green algae also occur. The grab stations were placed in the most favourable situations for *Micronecta* after a preliminary exploration with a hand net. This insect was also found in large numbers at depths of 2 and 3 ft. (0·6 and 0·9 m.) in thick filamentous green algae on a shingle spit.

Micronecta poweri is, therefore, found on all exposed shores in small isolated communities where local conditions afford some degree of shelter. It reaches its maximum abundance on moderately exposed sandy shores with thick vegetation, extends to the more exposed reed-beds, but disappears when organic matter begins to accumulate.

(2) *Tarns.*

Tarns fall conveniently into two classes according to the mode of origin: natural tarns of glacial origin, and artificial tarns formed by a recent artificial dam. The following natural tarns have been investigated: Low Water, Blea (Langdale), Sprinkling, Styhead, Lingmoor, Stickle, Codale, Easedale, Blea (Wythburn), Knott's Dock, Grisedale (Helvellyn) (Pl. 1, phot. 1), Red (Helvellyn), Scales and Bowscale. With the exception of Lingmoor Tarn, which has reached an advanced stage of evolution and has nearly filled up, all are barren of Corixids. Their stony shores, devoid of vegetation, are not suitable for the existence of these insects, which appear to require a soft substratum. On the other hand, the artificial tarns (Pl. 1, phot. 2) usually have a soft bottom of recently flooded, terrestrially formed, peat, and here Corixids are abundant.

It should be noted that every tarn from which records have been made is below 450 m. (1500 ft.) and the altitude factor, important in pools, does not call for consideration.

The following species of Corixids were recorded in tarns, the numbers in brackets indicating the number of stations at which each one was found. Records are taken from 63 stations in 37 tarns.

Sigara scotti	(42)	*Sigara venusta*	(4)
S. castanea	(26)	*S. limitata*	(2)
S. distincta	(23)	*Corixa geoffroyi*	(2)
Cymatia bonsdorffi	(21)	*C. dentipes*	(1)
Sigara linnei	(19)	*Sigara hieroglyphica*	(1)
S. fossarum	(15)	*S. semistriata*	(1)
S. praeusta	(12)	*S. nigrolineata*	(1)
S. striata	(8)	*S. wollastoni*	(1)
S. sahlbergi	(4)	*S. germari*	(1)
S. falleni	(1)		

The numbers of the species in the right-hand column never amounted to more than a few per cent. of the total population and they are not considered further. The distribution of the remaining species is shown in more detail in Tables 5 and 6.

Soil conditions in these tarns are less simple than in Windermere. In the first place the soil is of terrestrial instead of subaquatic origin, and is therefore somewhat different in character; in the second place it contains, at the beginning of the life of the tarn, about 50% of organic matter. This value may increase in the usual way or decrease owing to decomposition brought about by the deposition of silt. Although this makes the actual course of evolution more involved, the following important facts emerge. Table 5 shows 22 tarns set out with the Corixid fauna, the % o.m.s. and other details at one or more stations. The value at the station with the lowest % o.m.s. is used to arrange the tarns which are thus set out in order of descending minimum organic content. In any tarn there may be one, two or three of the following types of habitat:

(*a*) An area where the % o.m.s. is relatively low (8–50%). Such areas are usually near a stream mouth where there is a supply of silt which has enabled the original peat to be decomposed. These areas have a thick growth of vegetation made up of such plants as *Lobelia dortmanni*, *Myriophyllum* sp., *Callitriche* sp., *Potamogeton natans*, *Castalia alba*, *C. minor* and *Equisetum limosum*. The dominant species of Corixids in these areas are *Sigara distincta*, *S. fossarum* and *S. scotti*.

(*b*) An area where the % o.m.s. is relatively high (23–83%). Such areas are either places where the % o.m.s. has increased owing to silting having been arrested by the growth of plants, or places where the original peat has undergone little change. Typical plants are *Juncus fluitans*, *Apium inundatum*, *Utricularia* sp., *Menyanthes trifoliata*, *Potamogeton natans* and *Callitriche* sp. The dominant species of Corixid is *Sigara scotti*.

Table 5

Note. Habitat subdivisions (*a*) etc. refer to field survey data on specimen labels.

Tarn	pH of water	Vegetation at stations	% o.m.s.	Date	*S. scotti*	*S. castanea*	*S. fossarum*	*S. distincta*	*S. striata*	*C. bonsdorffi*	*S. linnei*	*S. praeusta*
Barngates Quarry	—	*Carex*	—	1 Apr. 1936	—	19	—	—	—	—	3	—
Whitemoss Reservoir	—	*Sphagnum*	—	27 Nov. 1935	—	16	—	—	—	—	—	—
Wray Mires Fishpond 1	5·8	(*a*) *Sphagnum* and *Juncus*	81	13 Jan. 1937	5	24	—	—	—	—	—	—
		(*b*) *Carex* and *P. natans*	83	13 Jan. 1937	30	—	—	—	—	—	—	—
Stephen How	—	*Menyanthes*	80	25 Mar. 1936	41	—	—	—	—	—	—	—
Wray Mires Fishpond 2	5·8	(*c*) *Iris*	78	13 Jan. 1937	2	11	—	—	—	—	—	—
		(*b*) *P. natans*	72	13 Jan. 1937	24	3	—	—	—	—	—	—
Wray Mires Fishpond 3	5·6	*Juncus*	77	13 Jan. 1937	1	25	—	—	—	—	—	—
Arnside	6·8	*P. natans*	71	9 Jan. 1937	28	—	—	1	—	—	—	—
Lingmoor	5·7	*Utricularia*	67	3 Oct. 1936	25	—	—	—	—	2	—	—
Gill Head Fishpond	6·6	*Littorella*	53	20 Feb. 1936	56	—	—	—	1	—	—	—
Wray Mires	6·8	(*b*) *P. natans*	50	15 Mar. 1936	11	3	30	9	—	—	—	—
		(*d*) Thin *Carex*	62	13 Nov. 1936	35	2	6	1	—	—	—	—
		(*a*) *Carex* and *Juncus*	85	17 Jan. 1937	2	31	1	—	—	—	—	—
Cleabarrow	6·8	*Carex*	48	4 Feb. 1937	22	—	—	18	—	—	—	—
School Knotts	7·0	(*a*) *Littorella*	44	7 Mar. 1936	16	3	—	—	—	—	—	—
		(*b*) *P. natans*	43	24 Feb. 1937	25	3	—	3	—	1	2	1
		(*c*) *Carex*	63	7 Mar. 1936	—	32	—	—	—	—	2	—
Wise Een Fishpond	6·8	*Littorella*	42·5	28 Oct. 1936	57	—	—	1	2	—	—	—
Three Dubs	6·4	(*a*) *Callitriche*	38	27 July 1936	112	7	—	—	—	—	—	—
		(*b*) *Juncus*	67	27 July 1936	5	7	—	—	—	—	—	—
Birket Houses	5·7	*Apium* and *Myriophyllum*	37	29 Feb. 1936	2	13	—	—	—	—	—	—
Lost	—	(*x*) *P. natans*	29·5	12 Nov. 1936	3	—	12	3	—	—	1	4
		(*z*) Bare mud	35·5	12 Nov. 1936	—	—	33	1	—	—	—	—
		(*y*) Thick *Carex*	70	12 Nov. 1936	—	11	—	—	—	—	14	—
Wise Een	6·9	(*c*) *Littorella*	29·5	28 Oct. 1936	19	—	—	—	—	—	—	—
		(*h*) Thin *Carex*	28	12 Feb. 1937	31	—	13	5	6	—	—	—
		(*i*) *Carex* and *P. natans*	32	12 Feb. 1937	18	—	17	9	—	—	—	—
		(*e*) Thick *Carex*	55	13 Nov. 1936	95	—	14	2	1	—	—	—
		(*b*) *Juncus*	89	28 Oct. 1936	19	15	—	2	—	—	—	—
Blelham Fishpond	—	(*a*) *Myriophyllum* and *P. natans*	—	23 Feb. 1936	—	—	17	—	19	—	—	—
		(*b*) *Juncus*	27	5 Oct. 1935	1	1	47	—	8	—	—	—
Green Hows Reservoir	6·7	*P. natans*	23	23 Sept. 1936	24	—	—	—	—	—	—	—
Moss Eccles	6·8	(*c*) Thin *Carex*	24	12 Feb. 1937	36	—	1	12	—	—	—	—
		(*d*) *P. natans*	64	11 Oct. 1936	22	—	2	1	—	—	—	—
Gill Head Reservoir	6·7	*J. fluitans*	12	20 Feb. 1936	67	—	—	2	—	3	—	—
Clay Pond	—	Bare mud	8	2 Oct. 1935	10	—	104	48	—	—	2	—

Table 6

Note. Habitat subdivisions (*a*) etc. refer to field survey data on specimen labels.

Tarn	*p*H of water	Vegetation at stations	% o.m.s.	Date	*S. scotti*	*C. bonsdorffi*	*S. linnei*	*S. praeusta*	*S. distincta*	*S. sahlbergi*	*S. fossarum*	*S. castanea*
Rather Heath 6	7·0	(*c*) Thin *Carex*	20	19 Dec. 1936	**23**	6	—	1	1	—	—	—
		(*d*) Thick *Carex*	42	19 Dec. 1936	—	**14**	2	2	—	—	—	—
Rather Heath 1	7·0	(*a*) *Apium*	—	29 Nov. 1936	**23**	4	—	—	1	—	—	4
		(*d*) *Carex*	49	19 Dec. 1936	—	**11**	3	6	2	—	**19**	—
		(*b*) *Carex*	—	29 Nov. 1936	1	**14**	4	—	—	—	1	—
Little Ludderburn	7·0	(*a*) Bare mud	76	11 Sept. 1936	**28**	—	—	—	—	—	—	—
		(*b*) *Callitriche*	68	11 Sept. 1936	8	**11**	—	—	2	—	—	—
		(*c*) *Carex*	—	29 Feb. 1936	—	**65**	—	—	1	—	—	—
New	7·0	*Callitriche* and *Juncus fluitans*	19·5	28 Sept. 1936	6	**19**	1	8	1	—	—	3
Slew	6·3	(*b*) *P. natans*	76	6 Apr. 1936	4	**44**	4	**24**	**37**	—	—	—
		(*a*) *Juncus*	73	7 Jan. 1937	—	**12**	2	—	5	5	—	—
		(*c*) *Carex*	90	7 Jan. 1937	—	2	**11**	—	—	—	—	—
Lindeth	6·9	(*e*) Bare mud	29	1 Jan. 1937	**29**	**12**	—	—	—	—	—	1
		(*c*) Thin *Carex*	73	1 Jan. 1937	**31**	5	1	3	—	—	—	1
		(*d*) Thick *Carex*	92	1 Jan. 1937	3	**12**	**11**	3	—	—	—	4
		(*b*) *Carex* and *Callitriche*	—	6 Dec. 1936	—	—	**30**	**16**	—	1	—	3
Rose Castle	—	*Carex*	69	19 Feb. 1936	—	5	**35**	—	—	—	—	5
Podnet	7·0	*Myriophyllum*	65	11 Sept. 1936	6	4	—	**13**	—	—	—	—
High Man	6·7	*Carex*	78	19 Mar. 1936	—	—	—	**16**	—	—	—	—
Robinson	5·8	(*a*) *Carex* and *J. fluitans*	—	6 Apr. 1936	5	—	2	—	—	—	—	**48**
		(*b*) *Carex*	—	17 Jan. 1937	9	—	**10**	—	—	—	—	**19**
Lost Tarn		See Table 1	—	—	—	—	—	—	—	—	—	—

(*c*) An area with a high % o.m.s. (37–89 %) and a thick growth of *Sphagnum* sp. or *Carex* sp. The dominant species is *Sigara castanea*.

The appearance of a thick bed of *Sphagnum* or *Carex* is clearly the last stage in the evolution of an aquatic habitat. *Sigara castanea* must, therefore, come after *S. scotti* in the evolutionary succession. With an increase in the % o.m.s. *S. scotti* replaces *S. distincta* and *S. fossarum* and there is, therefore, in tarns the following succession of Corixid species:

$$\left.\begin{matrix} \textit{S. distincta} \\ \textit{S. fossarum} \end{matrix}\right\} \rightarrow \textit{S. scotti} \rightarrow \textit{S. castanea}.$$

The figures shown in Table 5 appear to justify this general conclusion but the correlation between the values for the % o.m.s. and the species of Corixids found is not at all close. This is, perhaps, largely due to the absence of an accurate method of assessing the quality of a soil, that is, of obtaining a knowledge of the rate at which the % o.m.s. has increased. This factor, as indicated in an earlier paragraph, is dependent on the proportion of bases present. It seems likely that *S. distincta* and *S. fossarum* occur on soils with a low or moderate % o.m.s. only when a certain proportion of bases is present. Where the proportion of bases is very low *S. scotti* is the dominant species,

even though the % o.m.s. be very low also. Typically, such conditions are found in sandy-bottomed heathland localities, e.g. Little Sea, Studland (Diver and others); in the present area they are found in Gill Head Reservoir (o.m.s. 12%) which has a stiff clay bottom supporting an abundant growth of *Juncus fluitans*. Pearsall (1920, p. 194) has shown that this plant grows on soils which are poor in bases with either a very high or very low % o.m.s.

The boundaries between the territories of species, particularly *S. scotti* and *S. castanea*, are often quite sharp. Thus the two stations in Wray Mires Fishpond 1 were barely 1 m. apart, one in the middle, the other at the edge, of a thick bed of emergent vegetation. *S. scotti* is always more numerous than *S. castanea*.

In the tarns in Table 6 there is a different succession of species. *Sigara scotti*, *S. fossarum* or *S. distincta* are found in the less advanced areas of the tarn. In areas with higher % o.m.s. they are replaced by *Cymatia bonsdorffi* and in the thickest reed-beds *Sigara linnei* is the dominant form; *S. castanea* is found only in quite insignificant numbers. Another species, *S. praeusta*, is commonly found but its relation to the others is still obscure.

In geological and botanical features these are similar to the tarns already considered. The only apparent difference is that the present tarns receive organic matter from some external source; thus Rather Heath 1, Slew, Rose Castle, Robinson and Lost are surrounded by trees; Rather Heath 6 and New are sufficiently near trees to receive a large number of dead leaves every autumn; and Podnet and Little Ludderburn are recently dammed peat mosses each containing a number of drowned birches. Rather Heath 6 and Lindeth are fouled by poultry and High Man is fouled by ducks. Kjeldahl analyses show that the mud of these tarns has a relatively low carbon/nitrogen ratio (12·3 to 16·2, average 14·1) but this is not significantly lower than that of some of the localities where *S. fossarum* and *S. distincta* are found.

Four tarns have been omitted from the tables. Two of these resemble the rest and have a high o.m.s. (37 and 60%), but they are inhabited, one by *S. striata* alone, the other by *S. striata* and *S. falleni*, both species characteristic of habitats where the % o.m.s. is low. The remaining two are peculiar; both are old quarry workings with no inlet or outflow, 6–8 ft. of water and a vast quantity of dead leaves. *S. sahlbergi* is the only species found in them.

(3) *Pools*.

Pools are abundant all over the Lake District: 69 are considered in this paper. They may be classified into high pools and low pools, for it is found that the two have quite distinct associations of Corixid species. It will be convenient to use the Corixid fauna as the criterion distinguishing the two rather than to assign a given altitude as a rigid boundary between them.

Low pools. (Pl. 1, phot. 3). The highest is 450 m. above sea-level. Though most are quite small, some cover an area of several thousand square metres, but the depth seldom exceeds 1 m. The commonest plant is *Sphagnum,* but others such as *Menyanthes trifoliata, Juncus fluitans, Utricularia* sp., *Potamogeton natans* and *Carices* are sometimes found as well. The *p*H of the water ranges from 4·5 to 6·5. Analysis of seven bottom samples showed an organic content ranging from 42 to 82 % with an average of 75 %. The most intense colour of the water was only 15 units.

There are 35 pools altogether, and the following is a list of species of Corixid recorded, with the number of pools in which each one was found:

S. castanea	(24)	*C. geoffroyi*	(2)
S. scotti	(17)	*S. linnei*	(2)
S. praeusta	(5)	*S. striata*	(1)
S. nigrolineata	(4)	*S. distincta*	(1)
S. sahlbergi	(3)	*S. limitata*	(1)
S. venusta	(3)	*S. semistriata*	(1)
S. hieroglyphica	(2)	*S. fossarum*	(1)

S. castanea was dominant in 14, *S. scotti* in 12, and in two pools both species were equally abundant: no other species was found in significant numbers in any of these 28 localities. As in tarns, *S. scotti* occurs where vegetation is sparse or absent, *S. castanea* where vegetation is dense. The occurrence of these two species and no others in this environment with a high % o.m.s. confirms conclusions drawn from the study of tarns.

In the remaining seven low pools, *S. nigrolineata* is dominant in three and *S. praeusta* in two. Both these species fly readily from the sorting dish which suggests an explanation of their distribution; for all the pools are small and shallow and are probably temporary, though only one has actually been seen to dry up. *S. venusta* is dominant in two localities which differ somewhat from the rest. They are shallow quarry excavations with a depth of little more than 40 cm. of water and the bottom is covered with slates on which grows an algal felt.

High pools. (Pl. 2, phot. 4). The lowest is 400 m. (1300 ft.), the highest 800 m. (2700 ft.), and the majority about 600 m. (2000 ft.) above sea-level. In extent they range from two to two or three hundred square metres, and in depth from a few centimetres to about one metre. The bottom is of peat and has a high % o.m.s. Analysis of samples from ten pools showed an organic content ranging from 53 to 91 % with an average of 80 %. The carbon/nitrogen ratio of four samples ranged from 17·0 to 20·8. The water is seldom highly coloured and the number of units varies between 0 and 200; the *p*H ranges from 4·0 to 5·0, but is usually between 4·1 and 4·3. There are all stages between pools with no vegetation at all and pools completely overgrown with plants, such as *Sphagnum, Hypnum fluitans* and green algae.

Corixids are usually present and, though they are not abundant when compared with localities at lower altitudes, it is nearly always possible to collect between ten and twenty individuals. There are 34 pools, and the follow-

Phot. 3. Green Pool. *Sigara scotti* occurs in the open on the right, *S. castanea* in the *Carex* beds on the left.

Phot. 4. Seat Sandal. Habitat of *Corixa wollastoni*.

ing is a list of the species of Corixid together with the number of pools in which each was found:

S. wollastoni	(29)	*S. venusta*	(5)
S. nigrolineata	(27)	*S. castanea*	(2)
S. hieroglyphica	(12)	*S. scotti*	(1)
S. carinata	(8)	*S. praeusta*	(1)
C. geoffroyi	(5)		

in 32 out of the 34 *S. wollastoni* and *S. nigrolineata* or both were the only species which occurred in significant numbers and the proportions in which they were found were:

S. wollastoni %	Number of localities	*S. nigrolineata* %
0–10	10	90–100
10–20	1	80–90
20–30	3	70–80
30–40	1	60–70
40–50	1	50–60
50–60	1	40–50
60–70	3	30–40
70–80	2	20–30
80–90	1	10–20
90–100	9	0–10

The distribution of *S. wollastoni* and *S. nigrolineata* is evidently not random, but it is hard to make out what factors are concerned. Both species occur in pools with no vegetation and in pools with thick vegetation, so this factor, important in low pools, is not significant. Furthermore, it is unlikely that the nature of the soil or the water is important, for on six occasions it was found that of two pools lying close together in the same drainage area one was dominated by *S. wollastoni*, the other by *S. nigrolineata*. In five out of the six cases, however, the pool containing *S. nigrolineata* was distinctly smaller or shallower than the one inhabited by *S. wollastoni*. Further, isolated pools with *S. nigrolineata* tended to be smaller or were located in smaller drainage areas and this, linked with the observation that *S. nigrolineata* takes wing from a sorting dish more readily than *S. wollastoni*, suggests that these pools have dried up, and, being recently filled, are populated by the more active colonizer of the two species. It is hoped to investigate this suggestion by studying the invasion of artificially made pools.

In the remaining two pools *S. carinata* was dominant, and both were among the largest in the whole series. In one of them separate collections were made from the middle (depth about 0·5 m.) and from the edge. The catches were:

Middle	*S. carinata*	14	*S. wollastoni*	2	*S. nigrolineata*	1
Edge	*S. nigrolineata*	20	*S. carinata*	8	*S. wollastoni*	4

Both *S. carinata* and *S. wollastoni* are confined to the north of the British Isles, and may perhaps belong to the Alpine relict fauna. *S. nigrolineata* is common and widely distributed.

5. Acknowledgements

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6. Summary

1. The percentage of organic matter in a subaquatic soil has been shown by Pearsall (1920, 1921) to be an important factor in the distribution of certain species of plant. As the percentage of organic matter increases there is a succession of plant species. Different successions are found at different rates of increase of the percentage of organic matter.

2. The present investigation, carried out in the central and southern parts of the English Lake District, describes a similar relation between the soil and certain species of Corixidae.

3. Where the rate of increase of the percentage of organic matter in a soil is rapid there is the following succession of Corixidae:

$$\textit{Micronecta poweri} \rightarrow \textit{Sigara striata} \rightarrow \left\{\begin{matrix}\textit{Sigara distincta} \\ \textit{Sigara fossarum}\end{matrix}\right\} \rightarrow \textit{Sigara scotti} \rightarrow \textit{Sigara castanea}.$$

4. For the succession where the rate of increase of the percentage of organic matter in the soil is slow the evidence is scanty. *Sigara linnei* and *Sigara sahlbergi* appear to be the last two species in the succession.

5. In 11 tarns, however, there was a succession:

$$\textit{Sigara scotti} \rightarrow \textit{Cymatia bonsdorffi} \rightarrow \textit{Sigara linnei}.$$

A fourth species *S. praeusta* is associated, but its relation to the others remains obscure. These tarns appear to differ from the rest in that they receive organic matter from an external source.

6. In localities above about 450 m. there is a quite distinct association of species. *Sigara wollastoni*, *Sigara nigrolineata* and, in two cases out of 34, *Sigara carinata* were dominant.

REFERENCES

Diver, C., Macan, T. T., Walton, G. A. & Banks, C. J. "Contributions towards a survey of the plants and animals of South Haven Peninsula, Studland Heath, Dorset. No. 6. Distribution of Corixidae." (in-press).

Hutchinson, G. E. (1926). "Hemiptera-Heteroptera. pt. I. Hydrobiotica and Sandaliorrhyncha." In J. S. Gardiner, "The natural history of Wicken Fen," pt. 3: 234–52.

Moon, H. P. (1934). "An investigation of the littoral region of Windermere." J. Anim. Ecol. 3: 8–28.

Moon, H. P. (1936). "The shallow littoral region of a bay at the north-west end of Windermere." Proc. Zool. Soc. Lond. 491–515.

Ohle, W. (1934). "Chemische und physikalische Untersuchungen norddeutscher Seen." Arch. Hydrobiol. 26: 386–464.

Pearsall, W. H. (1920). "The aquatic vegetation of the English Lakes." J. Ecol. 8: 163–201.

Pearsall, W. H. (1921). "The development of vegetation in the English Lakes, considered in relation to the general evolution of glacial lakes and rock basins." Proc. Roy. Soc. (B) 92: 259–84.

Poisson, R. (1935). "Les Hémiptères aquatiques Sandaliorrhyncha Börn. de la Faune Française." Arch. Zool. Exp. et Gén. 77: 455–563.

Rankin, W. Munn (1911). "The lowland moors ("mosses") of Lonsdale (North Lancashire), and their development from fens." In "Types of British vegetation", ed. by A. G. Tansley: 247–8.

THE ROOK (*CORVUS FRUGILEGUS*) POPULATION OF NORTH-WEST DENBIGHSHIRE

By M. MITCHELL

A PRIMARY survey of the area was made during the winters of 1934–35 and 1935–36. The actual census of nests was taken between 15 and 28 April 1936.

1. *The area.*

This consists of 112·75 sq. miles. It is defined on the north by the coast from the river Conway to the river Clwyd; on the east and south, to Llanfairtalhairn by the river Elwy, and from Llanfairtalhairn to the bridge over the Conway at Llanrwst by the Abergele-Llanrwst road; on the west the area is bounded by the river Conway. It varies in character, rising from sea-level to a height of 1298 ft., but may very roughly be divided into three regions: the coast, the river valleys and a stretch of moorland, much of which is 1000 ft. or more above sea-level.

Geologically the area is made up largely of limestone and shales. While lying for the most part in Denbighshire, very small regions of both Flint and Caernarvonshire are included in the area taken.

2. *Possible errors.*

(*a*) The birds may not have finished building by 28 April, but this is unlikely. (*b*) Nests may have been destroyed. (*c*) Mistakes in actual counting. This seems the most likely source of error though mistakes might tend to equalize. Where possible counts were checked by an independent helper.

3. *Results.*

Total area 112·75 sq. miles	Rooks per acre of cereals 1·84
Total nests 1571	Rooks per acre of roots 0·36
Nests per square mile 13·93	Rooks per acre of total arable land 4·52
Nests per square mile of agricultural land 18·7	Acres of agricultural land per nest 34·09

These figures are approximate, having been extracted in parishes, while the boundaries taken do not coincide exactly with the parish boundaries.

4. *Discussion.*

For the purpose of the census all sites exceeding a distance of approximately a quarter of a mile from one another have been termed rookeries.

Suggested factors influencing distribution.

(*a*) *Water.* 75% of the rookeries were within 250 yd. of a water supply of some sort.

(*b*) ***Buildings.*** 75% of the rookeries were within 200 yd. of buildings, although in several cases the rookery antedates the buildings.

(*c*) ***Altitude.*** No rookeries occur above 600 ft. Approximately one-third of the area is more than 600 ft. above sea-level.

(*d*) ***Trees.*** Elm, sycamore, oak, beech and pine are the species used, all extensively, though there appear to be more nests in elms than in any of the other trees.

(*e*) *Competition.* At the higher altitudes the rook appears to be replaced largely by the carrion crow (*Corvus c. corone* L.).

(*f*) *Distance apart of rookeries.* It is not the case in this district, as is suggested by Marples (**1**) working in the Wirral Peninsula, that rookeries tend to be spaced about a mile apart.

5. *Summary.*

Density of nests 13·93 per sq. mile. Preference seems to be shown for a site near water, although evidence on this point is not conclusive. Altitude appears to be a governing factor, there being no nests above a height of 600 ft. above sea-level.

6. Acknowledgements and thanks are due to the Statistical Branch of the Ministry of Agriculture and Fisheries; to the Borough Surveyor of Colwyn Bay; and to the many landowners who have made the taking of this census possible.

REFERENCE

1. **Marples, B. J. (1932).** "The rookeries of the Wirral Peninsula." J. Anim. Ecol. 1: 3–11.

THE FIELD MICE OF ICELAND

By PATRICIA LUPTON and URSULA WYKES

(*With* 1 *Map in the Text*)

1. Introduction

While we were planning an ecological expedition to Iceland in 1935, Mr Charles Elton suggested that a collection of Icelandic field mice should be made in order to compare them and their parasites with the species occurring in England, the Hebrides and Scandinavia, which have been the subject of surveys during recent years (Elton *et al.* 1931; Elton, 1934, 1936; Hora, 1934).

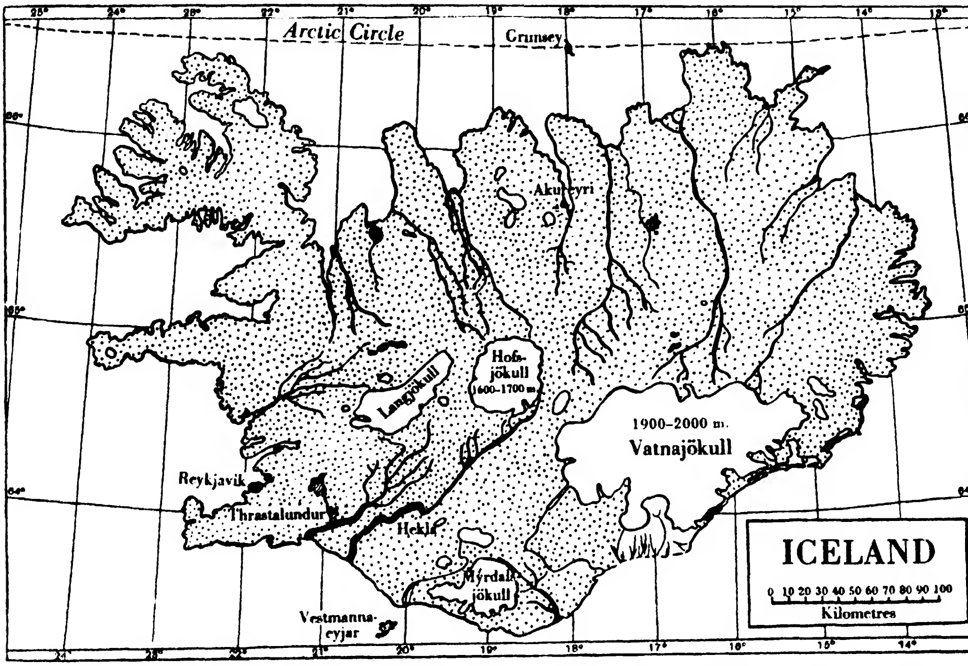
Although *Apodemus* is one of the few mammals indigenous to Iceland, very few references to it can be found in any scientific literature. Pennant (1792) mentioned that mice were plentiful in Iceland in the woods of Husafels. G. S. Miller (1912) in his catalogue of the mammals of western Europe includes under *Apodemus sylvaticus sylvaticus* six specimens from Iceland which are now in the U.S. National Museum. Mice are occasionally mentioned in Saga and travel literature, for example in the Floamanna and Biskopa Sagas which were composed in the latter half of the thirteenth century. The following passages from the Biskopa Saga indicate that, even at that time, mice were occasionally so plentiful as to be regarded as a plague:

> I, 194. There was such a plague of mice [in a small cottage] that she could hardly stay there.
>
> I, 293. Mice destroyed the corn and crops, and the ground in all parts there was hollow and full of mice [on an island called Videy].

Rats were distinguished from mice as *mýss valskar*, that is, foreign mice. Eggert Olafsen, himself an Icelander from the north-west coast, & Povelsen (1805) in their "Travels in Iceland" give the following account which seems to us so delightful as to be worthy of full quotation:

> There is but a small number of mice in Iceland, and the white mouse of the woods (*Mus sylvaticus*) appears to be only a variety of a domestic mouse. The instinct of this little animal induces it to collect a quantity of grain for its winter provender; and its magazines may be frequently discovered in the woods and outskirts. We are assured, that these mice undertake long journies, and even cross rivers, on which occasion they have the sagacity to pass the water in a diagonal line: they use pieces of dry cow-dung for rafts, which they load with grain on their return. The number attached to one of these rafts is from four to ten, and each of them assists in launching it. It is also curious, that they swim on each side, and their faces are opposite, while their tails serve for rudders. These voyages are not always successful, for sometimes their boats sink, when they save themselves by swimming with wonderful ingenuity. These curious circumstances were detailed to us by persons of credit, who had had ocular demonstration of the fact.

These references to the abundance of mice in early times discredit the opinion held by Hooker (1813) that "The few rats and mice, that are said to exist here, are brought by ships from other countries". The systematic position of the Icelandic mice will be discussed in a later section.



Map of Iceland showing location of Thrastalundur. Ice-caps white, lakes cross-hatched.

2. METHODS OF SURVEY

Birch-scrub (*Betula nana*), which is very common in certain localities in Iceland, seemed to provide the most probable habitat and for this reason we chose the district around Thrastalundur, Sogsbru, for our trapping activities. Thrastalundur lies on the eastern bank of the river Sog, some 70 km. east-south-east of Reykjavik, and at a height of 14 m. This region is composed chiefly of *Apalhraun* or block lava and is therefore extremely hillocky. It is colonized by *Betula nana*, reaching an average height of 60 cm., *Salix lanata*, *Cassiope hypnoides* and various species of grasses. The total area of scrub is approximately 2 sq. km. and covers part of the lava field of Hekla.

The trapping was done during the first week in August, by which time the short Iceland summer was already nearly over and night and day could be definitely distinguished. Break-back traps were used and each night 50–100 were set in groups of 5, 10, or 15 in different areas of scrub. They were placed as far as possible near mouse runs but these were often not very obvious and the holes were hidden in the cavities below blocks of lava. The traps were baited with cheese, and oats sprinkled round them. We visited the traps morning and evening and put the mice caught into separate canvas bags. We found mice

caught in the traps only in the morning which indicates that their habits are mainly nocturnal even during the summer months. The average catch of mice was not large, varying between one and ten a night, but the weather was so consistently wet that this was not surprising. The majority of mice were dead when found. Those which were still alive were killed with chloroform. Unfortunately no record was kept of the mice which were killed in this way, so that it is not possible to say whether they produced a higher percentage of parasites.

The fur of each mouse was examined carefully for ectoparasites which were preserved in alcohol. The skin was then removed, treated with arsenic-borax powder and preserved as a flat or "cased" specimen. The skins and skulls have been numbered B.A.P. 46 to 76 in accordance with the series of specimens of *Apodemus* sp. in the possession of the Bureau of Animal Population at Oxford, where the collection is provisionally deposited.

3. Measurements

Thirty-one mice were caught, of which 24 were males and 7 females. The body length, tail length, and total weight of each individual are given in Table 1. The weights of females may be subject to an error due to embryo weights not having been recorded. The parasites include 11 species of mites (Acarina) and one flea (Aphaniptera). For their distribution on different individuals reference should be made to the table.

4. Parasites

The most interesting point which emerges from a comparison of the parasites of the Icelandic mice with those of Continental and British species concerns the fleas. It appears that the Icelandic species is *Ctenophalmus agyrtes agyrtes* (Heller). This subspecies is widely distributed on the Continent, having been found in Norway, Germany, Austria and Switzerland. Another subspecies, *C. agyrtes* var. *celticus*, occurs in Great Britain and Brittany and has been found elsewhere in France. Since the fleas on these Icelandic mice belong exclusively to the subspecies *C. agyrtes agyrtes* it would seem that the mice must have been derived originally from the Scandinavian stock rather than that of Great Britain or its islands.

5. Status

The status of *Apodemus islandicus* has not been finally ascertained, and a full discussion will not be attempted here, since the Zoological Museum at Copenhagen will be publishing soon a report on the systematic position of the species, partly based on the materials loaned to the Museum by us. The general appearance of this form is, however, against it being simply an ordinary European wood mouse that has recently been transported accidentally to

Iceland. In its large size and rather brilliant coloration, the form resembles more *A. hirtensis* of St Kilda, and it may well be that it has been isolated upon Iceland for a very long time.

Table 1. *Measurements of mice and distribution of their parasites, Thrastalundur*, 1–6 *August* 1935

					Parasites												
					Acarina										Aphaniptera		
No. of mouse	Sex	Weight (g.)	Tail length (cm.)	Body length (cm.)	Tyroglyphidae	*Myobia musculi* Schrank	*Myonyssus gigas* Oudms	*Nothrus sylvestris* Nic.	*Nothrus palustris* Koch	*Pergamasus crassipes* L.	*Asca affinis* Oudms (deutonymph)	*Eugamasus furcatus* Can	*Haemogamasus michaeli* Oudms	*Eulaelaps stabularis* Koch	*Laelaps festinus* Koch	*Ctenophthalmus agyrtes agyrtes* ♀ Heller	*Ctenophthalmus agyrtes agyrtes* ♂ Heller
1	♀	17·6	7·9	9·1	—	—	—	—	—	—	—	—	2	4	8	—	—
2	♂	23·3	8·9	10·2	—	—	—	—	—	—	—	—	—	—	5	1	1
3	♂	35·17	9·8	9·2	—	—	—	—	—	—	—	—	—	1	4	6	5
4	♂	24·74	8·0	10·5	—	—	—	—	—	—	—	—	—	1	18	—	—
5	♀	30·20	10·2	10·8	—	—	—	—	—	—	—	—	1	—	2	—	—
6	♀	23·7	9·7	9·7	—	—	—	—	—	—	—	—	—	—	1	—	—
7	♂	22·9	8·7	10·6	—	—	—	—	—	—	—	—	1	—	17	—	—
8	♀	32·0	10·2	10·8	—	—	1	—	—	—	—	—	—	—	4	—	—
9	♂	35·0	10·1	10·5	—	—	—	—	—	—	—	—	—	—	14	1	1
10	♂	18·18	8·5	8·6	—	—	—	—	—	—	—	—	—	—	28	—	1
11	♂	36·1	9·0	11·2	—	5	—	1	—	—	—	1	—	—	19	3	—
12	♂	18·72	7·9	9·0	1	—	—	—	—	—	—	1	—	—	1	—	—
13	♂	18·7	9·6	9·2	—	—	—	—	—	—	—	—	—	—	14	3	—
14	♂	23·4	8·6	10·3	—	—	—	—	—	—	—	—	2	—	6	—	—
15	♂	20·1	8·9	8·5	—	—	—	—	—	—	—	—	—	4	2	—	—
16	♂	9·9	6·1	7·6	—	1	—	—	—	—	—	—	—	—	8	—	—
17	♂	26·0	8·6	9·4	—	—	—	—	—	—	—	—	5	5	20	2	1
18	♂	20·6	7·9	9·5	—	—	—	—	—	—	—	—	—	—	21	—	—
19	♀	19·7	8·1	9·1	—	—	—	—	—	—	—	—	—	4	9	3	3
20	♂	28·0	9·2	11·1	—	—	—	1	—	—	—	—	1	2	10	1	—
21	♂	21·8	8·6	10·1	—	—	—	—	—	1	—	—	—	—	22	2	4
22	♂	9·2	5·4	7·1	—	—	—	—	1	—	—	1	—	—	16	—	—
23	♂	9·3	4·5	7·0	—	—	—	—	—	—	—	—	—	5	8	—	—
24	♂	20·4	7·8	9·4	—	—	—	—	—	—	—	—	—	—	6	—	—
25	♂	33·0	9·6	10·7	—	—	—	—	—	—	—	8	—	2	27	5	6
26	♂	34·4	9·2	10·8	—	—	—	—	—	1	1	—	—	—	35	2	2
27	♂	17·1	7·9	8·3	—	—	—	—	—	—	—	—	—	—	18	—	—
28	♂	28·1	broken 4·9	10·3	—	—	—	—	—	—	—	—	3	4	17	2	—
29	♂	27·1	8·6	9·3	—	—	—	—	—	—	—	1	—	4	11	—	—
30	?	9·4	6·2	6·5	—	—	—	—	—	—	—	1	—	1	20	—	—
31	?	10·2	7·5	6·7	—	—	—	—	—	—	—	3	—	—	—	—	—

6. Acknowledgements

First and foremost we would like to thank Mr Charles Elton for his continual help and interest. We are much indebted also to Mr F. J. Cox and Mrs M. Hughes who undertook for us the identification of the fleas and mites respectively. The references to Saga literature were supplied by Prof. E. V. Gordon to whom we are very grateful.

7. Summary

1. A collection of Icelandic field mice was made in order to compare them and their parasites with the species occurring in Great Britain and Scandinavia.

2. The sex, weight, body length and tail length and ectoparasites of each individual were noted. The skulls and skins were preserved and are provisionally deposited in the Bureau of Animal Population at Oxford.

3. The subspecies of Aphaniptera found on the Icelandic mice, *Ctenophalmus agyrtes* var. *agyrtes* is widely distributed on the Continent and in Scandinavia but differs from the typical British species, *C. agyrtes* var. *celticus*. This suggests that the mice of Iceland were originally derived from the Scandinavian rather than the British stock.

4. The systematic position of *Apodemus islandicus* is being investigated by the Zoological Museum, Copenhagen, partly on the basis of this material.

References

Elton, C. (**1934**). "Metazoan parasites from mice in the Isle of Lewis, Outer Hebrides." Parasitology, 26: 107–111.

Elton, C. (**1936**). "Parasites from rodents and shrews in the Outer Hebrides." Ent. Mon. Mag. 72: 31–34.

Elton, C., Ford, E. B., Baker, J. R. & Gardner, A. D. (**1931**). "The health and parasites of a wild mouse population." Proc. Zool. Soc. Lond.: 657–721.

Hooker, W. J. (**1813**). "Journal of a tour in Iceland in the Summer of 1809," London, 2nd ed., Vol. 1, pp. 51–2.

Hora, A. M. (**1934**). "Notes on mites collected from the Isle of Lewis, Outer Hebrides." Parasitology, 26: 361–365.

Miller, G. S. (**1912**). "Catalogue of the mammals of Western Europe..." Brit. Mus., London.

Olafsen, [E.] & Povelsen [B.]. (**1805**). "Travels in Iceland." In "A Collection of Modern and Contemporary Voyages and Travels," London. 1806. Vol. 2, p. 58.

Pennant, T. (**1792**). "Introduction to the Arctic Zoology." London, 2nd. ed., p. lxx.

NOTES ON THE ANIMAL ECOLOGY OF BEAR ISLAND

By G. C. L. BERTRAM and DAVID LACK

(*With Plates* 3 *and* 4, *and* 1 *map*)

CONTENTS

PART I. GENERAL DESCRIPTION

1. INTRODUCTION

IN 1921 Summerhayes & Elton (**28**) visited Bear Island, and thus started a series of investigations by British expeditions on the ecology of Arctic regions, followed up in Spitsbergen by Summerhayes & Elton (**29**), in West Greenland by Longstaff (**23**), in Central Iceland by Anderson & Falk (**11**) and on Akpatok

(Ungava Bay) by Davis (**17**). Reference should also be made to later work in East Greenland by Madsen (**24**) and Jørgensen (**21**). The present paper may be regarded as in the same series, and describes our work on Bear Island between 20 June and 10 August 1932.

The collections have been presented to the British Museum (Natural History), and a duplicate collection of insects to the Hope Department of Entomology, Oxford University.

2. Topography and geology

The general account of the present expedition (**3**) includes a description of the island. Horn & Orvin (**20**) give a detailed account of the topography and geology, and Summerhayes & Elton (**28**) of the botanical habitats. Hence only a brief description is given here.

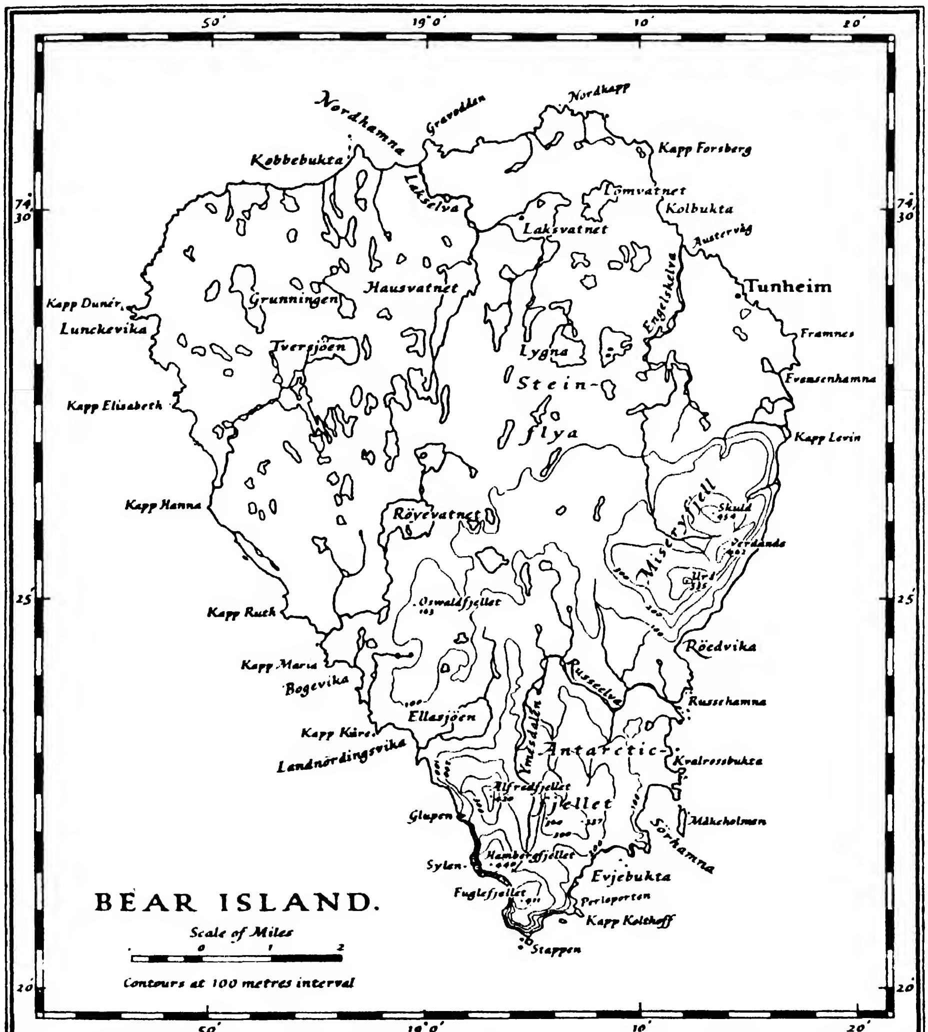
Bear Island (see map, Fig. 1) in the Barents Sea in Lat. 74° N., and Long. 19° E., is one of the most isolated islands in the Arctic, the nearest land being Spitsbergen, 120 miles to the north, while Norway is 240 miles to the south. It is some 12 miles from north to south and 9 from east to west. Geographically it can be divided into three main regions. The northern half of the island is a plateau at about 100 ft. above sea-level, flat in the west, gently undulating in the east, with a central rather higher area, the Steinflya. This region is covered with a network of shallow lakes (Pl. 3, phot. 1). The second region, in the east, is Mount Misery, a plateau mountain with three peaks, the highest about 1770 ft. The third region is the southern mountains, the Antarctic Range and several other peaks, all rather lower than Mount Misery, and in many places terminating seaward in steep cliffs. The highest of these has a sheer drop of 1400 ft. This southern region has only a few lakes.

The oldest geological formation is the Hekla Hoek, found in the southern dolomite cliffs and across Mount Misery. Unconformably on these are Upper Devonian strata followed by the Culm. These are chiefly sandstones, with a few coal seams, and come to the surface over much of the north and east of the northern plateau. Middle and Upper Carboniferous limestones occur in the southern region and also in the west of the northern plateau, and Triassic sandstone occurs on the peaks of Mount Misery. In general the limestones make a fairly smooth walking surface, but in the sandstone areas the loose boulders varying from a few inches to several feet across make walking difficult (Pl. 3, phot. 2). In some places these boulders encircle clay centres forming polygons.

3. Climate

Considering its high latitude, Bear Island has a comparatively equable maritime climate. Horn & Orvin (**20**) give the average monthly temperatures as January, −9·4; February, −11·2; March, −11·0; April, −7·6; May, −2·3; June, +1·7; July, +4·2; August, +3·6; September, +1·9; October, −1·7; November, −6·3; December, −7·5° C.

A branch of the Gulf Stream flows along the west coast, but a cold current from the north flows down the east coast. As a result, the island is covered with thick fog almost continuously throughout the summer. For example, during our stay of 52 days only five were clear and sunny, and for an aggregate of



Reproduced by permission of the Royal Geographical Society, from "The Geographical Journal," January 1933.

Fig. 1. Map of Bear Island.

about 21 days visibility was limited to 30 yd. Hence the climate is extremely humid.

Drift ice has been recorded round the island in every month, especially between February and May, but it is rare between May and September. The highest point, below 1800 ft., is not sufficient to induce abundant snowfall, so

that areas may sometimes remain snow-free in late autumn and winter. The ground is permanently frozen below about 0·75 m. (**20**, p. 12), so causing the run-off of water to be extremely rapid. The ground water used by plants can therefore contain only extremely small quantities of mineral salts.

The midnight sun lasts from 30 April to 13 August.

4. Flora

The flora of Bear Island is rather poor compared with that of Spitsbergen to the north (**26**, **28**, **29**). Bear Island possesses only some 53 species of Phanerogams, Spitsbergen about 127. This difference is correlated with the very different climatic conditions in some parts of Spitsbergen, where, particularly at the heads of the fjords, bright sun and high summer temperatures are recorded. Summerhayes & Elton have divided Svalbard (the modern Norwegian name for Spitsbergen and Bear Island) into four botanical zones; and although Bear Island is the most southerly part of Svalbard, it is placed in the most barren zone, characterized by the absence of *Dryas*, *Cassiope* and *Empetrum*. In some respects, however, Bear Island is more akin to the richer zones, and it possesses two species of Phanerogams (*Hippuris vulgaris* and *Rhododendron lapponicum*) and several more southern mosses which have not been recorded from Spitsbergen.

Summerhayes & Elton (**28**) have classified the plant communities, and the following summary is based primarily on their account. Fjaeldmark occupies most of the dryer parts of the island. This very open community consists mainly of Phanerogams; chiefly scattered individual plants, with a fair proportion of mosses and lichens. *Saxifraga oppositifolia* and *Salix polaris* tend to be the dominants. Many areas, particularly in the sandstone boulder region, are almost devoid of plants. Especially in sheltered places on the limestone of the northern plateau, a closed community, Herb Mat, is found, but the areas it occupies are extremely circumscribed. A closed moss vegetation (in our collections we did not distinguish between Summerhayes & Elton's Moss Heath and Moss Mat) tends to occur in damper, more sheltered areas than the Herb Mat. Here mosses predominate, and lichens are numerous.

Some of these areas tend to dry up later in the summer, being thus distinguished from Summerhayes & Elton's Wet Tundra, which remains damp. The most distinct division of the last is the closed vegetation consisting almost entirely of mosses which surrounds many of the lakes, and sometimes the streams, particularly in limestone areas. This community is often submerged for considerable periods after the snow melt.

The abundance of mosses and lichens on Bear Island is probably correlated with the almost continual damp fogs in summer, and is in contrast with the comparative scarcity of these plants in dry, sunny parts of the Arctic.

Though the above plant communities can be defined, it should be stressed that in practice they are not usually clear-cut divisions. Furthermore, a plant

succession, when it occurs at all, would seem to proceed extremely slowly in the unsatisfactory conditions provided for plant growth. As an example of how slowly plants colonize, in 1899 Lerner levelled some ground as a road between Sörhamna and Walrus Bay. Thirty-one years later that road was still clearly marked, and had been colonized by extremely few plants, mainly *Saxifraga oppositifolia*.

5. Manuring by sea birds

Where, as in the Arctic, the nitrogen supply in the soil is extremely low, any additions will have a most marked effect. Such additions are supplied locally by the sea birds, and since these birds feed at sea, the nitrogen which they deposit in droppings is a constant additive factor, and the faeces add appreciably to the actual bulk of the soil. The effects of bird manuring on the vegetation in Spitsbergen have been discussed in detail by Summerhayes & Elton (**29**) and Scholander (**27**).

On Bear Island the most marked effects occurred on ledges, and on slopes not so steep as to fail to retain the dung, below cliff colonies, especially of kittiwakes and guillemots. Here occurs the most luxuriant vegetation on the island, consisting almost exclusively of *Cochlearia*. On the unmanured cliff tops these plants were closely appressed to the ground and the leaves were typically less than 2 in. long. Below the kittiwake colonies growth was luxuriant, and the leaves up to a foot in length. On the damp cliff faces, manuring seemed also to assist the growth of *Enteromorpha*. On the other hand, too great manuring seemed to stultify the vegetation, as by some of the guillemot colonies and in the immediate neighbourhood of the more crowded kittiwake nests. It was also interesting to find at Tunheim a good growth of *Cochlearia* below what had, some 8 years before, been a miners' lavatory which opened directly over the cliff.

A second effect of manuring was the production of a closed Grass Mat. This would seem to be a divergence from the normal Herb Mat of Bear Island, and was found only in connexion with manuring in dry areas. It occurred as a rather narrow margin on the dry flat cliff top above glaucous gull colonies. The latter birds are in the habit of standing in numbers on the cliff top above their nests. There was also a much larger area round the huge glaucous gull colony at Cape Dunér (Pl. 4, phot. 3). "Skua hummocks" (**28**), found scattered in the fjaeldmark where arctic skuas perched or nested, were sometimes composed predominantly of Grass Mat.

In addition to these prominent effects, manuring on a smaller scale resulted in a general increase of the vegetation in certain areas. Thus the islet in Laksvatnet, where many arctic terns and eiders nested, had a richer vegetation than the neighbouring fjaeldmark, as had many of those "skua hummocks" which did not attain the state described above. Most of the scree slopes were almost devoid of vegetation, the chief exception being those beneath the inland colonies of puffin and little auk on Mount Misery. In some of these sloping

cliff areas a closed vegetation of mosses and *Cochlearia* had developed. Finally, certain of the lake margins were extensively resorted to by glaucous gulls and kittiwakes for bathing and resting, resulting in a richer development of the moss margin. In a few places this manuring had been so intense as to retard the growth of mosses.

6. Extent of the 1932 survey

Observations and collections of the fauna were extended to all the important land and fresh-water habitats, and during a stay of 7½ weeks it was possible to work many samples of each type. Attention was concentrated on the Vertebrates and Arthropods, but among the latter the Tardigrades and the insect parasites of mammals and birds were omitted. Apart from the nesting sea birds, marine life was not studied.

Tunheim in the north-east was used as a base, from which journeys were made all over the island, though the north and east were naturally worked more frequently than the south and west. The present survey is the most complete yet made, for previous zoologists had visited only circumscribed areas and for short periods, most of such visitors being on their way to or from Spitsbergen. The most important previous visits were that of the Oxford University Expedition of 1921 (**28**) which stayed 10 days in June in the south, and that of Thor (**30**) who stayed about a week at the end of July 1928 at Tunheim.

The summer of 1932 came extremely late. The land did not become snow-free until a day or two before our arrival, and drift ice was said to have been round the island until 10 days previously. Consequently observations could be made from the beginning of summer, which assisted the completeness of the survey. However, it is quite possible that, especially considering the lateness of the summer, a number of insects did not emerge until after our departure on 10 August, or perhaps not at all in 1932. Thus no adult *Prosimulium ursinum* were captured though larvae and later pupae were not uncommon, and hence it is possible that other Diptera with less conspicuous larvae might have been overlooked in 1932.

A complete list of the Vertebrates and Arthropods known from the island is given as an Appendix. In addition to adding many new forms to the island list (for details of which see the papers on the special groups, References A), the 1932 collection included nearly all the Arthropods (omitting some doubtful forms) found by previous collectors, except in the case of the mites (Acarina). The last were missed presumably through inexperience in collecting, though hundreds of specimens of certain species were brought back. For the mites, Thor's list (**30**) has been primarily used.

The ordinary methods of collecting were used, a sucking tube being the most valuable instrument for the larger insects, and a simple modification of the Berlese funnel for the Collembola and mites living in vegetation.

Phot. 1. The northern, lake-covered area.

Phot. 2. Steinflya—the central stony desert, a region almost devoid of vegetation.

BERTRAM AND LACK—BEAR ISLAND

PART 2. ECOLOGICAL DISTRIBUTIONS

7. THE FRESH WATERS

General notes

Owing to the small size of the island, none of the streams and rivers are large. They run fastest after the snow melt, and some of them dry up later in the summer. Apart from the larvae and pupae of *Prosimulium ursinum* and various Chironomidae, they contain almost no animal life.

Lakes and ponds are extremely numerous on the northern plateau, (Pl. 3, phot. 1) where they are all shallow (apparently none more than 21 ft. deep), and there are a few in the southern mountains, the most important being Ella Lake which is said to be 140 ft. deep. There are no brackish lakes nor any that can be considered of a relict type, such as occur in Spitsbergen.

The lakes fall into two main types. Those on the sandstone had an average *p*H of 6 (with little variation), their shores are usually devoid of vegetation and their bottoms consist of bare boulders. Those on the limestone had a *p*H of about 7·5 in the absence of sea bird manuring and marginal vegetation (which usually go together); but in the presence of these two the *p*H rose above 9, a high figure; the surrounding vegetation is typically a partially submerged closed moss bog, the bottom being usually covered by grey mud. Other lakes are intermediate between these two types, and thus a wide variety of conditions are represented. The extremes of *p*H were 5·6 in a sandstone lake, 9·6 in a manured limestone one.

On Bear Island, once the winter's ice has melted, the shallow fresh-water lakes rapidly tend to reach a temperature at which they are in radiative equilibrium with the heat received from the sun. However, as a result of the oceanic and atmospheric conditions in the neighbourhood, the air temperature over the island remains low, the average for July, the hottest month, being 4·2° C. Thus a peculiar state is reached in which the lakes are maintained at a temperature several degrees higher than that of the air. Of 43 readings in various lakes, the following are typical. On our arrival on 20 June nearly all the lakes still bore ice. As early as 26 June the temperature in Mosevatnet (a small lake in the north) was as high as 7·2° C. A small pond, measured 3 days later, was 1·5° C. at one end, while ice was still melting in another part. As early as 7 July a third had reached 9·5° C., and from now on most of those recorded were between 7 and 9° C. The larger lakes were slower to warm up, and were usually rather below this. As a check, the temperature was taken of the water in a deep pit (sunk in the coal mining days) which, being of small surface area, received proportionately little radiation. On 21 July the temperature here was only 1·5° C. It may be noted that the shallowness of most of the lakes (except Ella) and the frequent winds favour complete mixing of the waters and the absence of a temperature gradient. Summerhayes & Elton (**28**, p. 272) recorded temperatures in one Spitsbergen lake.

Collections of fresh-water animals were made in all the main types of lakes, the only omission being that, owing to lack of a boat, collections from Ella lake were limited to near the shore.

Lake fauna

(*a*) *Vertebrates*

The birds have been reported on in detail elsewhere (**4**). A number of ducks used the lakes, and waders and geese the lake and river margins, for resting and feeding when on migration. Omitting these, and also the uncommon breeding species, two species of duck, the long-tailed (*Clangula hyemalis*) and the eider (*Somateria mollissima borealis*) used the lake islets for breeding, but the eider was the only common species. The latter take their young to the sea when hatched, and Coward (**15**) states that the duck does not feed during incubation. The only common wader was the purple sandpiper (*Calidris m. maritima*) which fed chiefly on Chironomid fly larvae in the moss of the lake margins and probably at times on land insects. In June these birds were observed far out on the lakes picking through cracks in the fragmenting ice, presumably for Chironomid larvae, the only sizable animals in the plankton at that time. The red-throated diver (*Colymbus stellatus*) at times fed its young on the arctic char (*Salvelinus alpinus*), as did the two pairs of great northern diver (*C. immer*); but many of the lakes frequented by *C. stellatus* did not contain char, so that the birds fed at sea. Finally the arctic tern (*Sterna macrura*) also used the lake islets for nesting. These birds obtained most of their food at sea by diving, but they were also seen skimming Chironomid larvae and probably *Lepidurus arcticus* from the surface of the lakes, and occasionally hawked for adult Chironomidae in the air—three very different types of feeding. Hence although in some cases the lakes supplied a part of the food (possibly most or all for *Colymbus immer*), the birds chiefly frequented them for nesting on the islets, where they were safe from the arctic fox.

The arctic char (*Salvelinus alpinus*), the only species of fresh-water fish, occurred in many of the lakes, chiefly those connected with the streams and rivers. The fish apparently reach other lakes by temporary communications during the snow melt. On Bear Island, adults are found throughout the year, and in winter are caught in large numbers through holes in the ice. The stomachs examined contained nothing but large numbers of Chironomid larvae. For what little is known of the biology of this fish, see Dahl (**16**).

(*b*) *Arthropods*

As on land, the bulk of the fauna consisted of Arthropods. One water mite, *Sperchon lineatus*, was found on stones in the bottom of some of the lakes, and Thor (**30**) states that it is abundant in thick moss at the sides of the rivers.

The most conspicuous element in the insect fauna is the huge number of Chironomid fly larvae, which occur on stony and mud bottoms, in the thick

moss at the lake and stream sides and in the lake plankton. From a determination of the adults, 26 species of Chironomidae have been recorded from Bear Island (**6**), but not all of these have aquatic larvae. However, their life histories have not been worked out, so details cannot be given. Despite the large number of individuals which were collected, several species of Chironomidae were represented by only a few individuals and seemed very local (see Edwards (**6**) and Appendix 1). The only other group of Diptera were the Simulidae. The larvae of *Prosimulium ursinum* were found in several fast-running rivers and streams, but only in those which had come from lakes, presumably since only in these was there sufficient planktonic food. One species of caddis, *Apatania arctica* was found, the cases of sand and small stones being found on the rock and silt bottoms of the larger lakes (**7**).

Of the fresh-water Crustacea, which are very abundant in number of individuals, 15 species have been recorded, of which 6 were common. The occurrence of the various species over the island is erratic. Thirteen species were collected in 1932, and in only 15% of the collections were more than three species taken together in any one lake or pond. The greatest number of species in any one pond was five, found only once. Attempts were made to correlate the specific distributions with environmental factors such as the *p*H, the nature of the bottom and the amount of sea-bird manuring, in most cases with little success. There seems to be no summer cycle of dominant species; but further details need not be recorded here, since they have been already published (**2**).

8. Other invertebrates

No fresh-water Mollusca or Planaria are known from Bear Island. Non-Arthropod groups were not collected in 1932, but some information on the Rotifers and Enchytraeid Oligochaetes may be obtained from Summerhayes' and Elton's account of the Island, with which the present paper is in some ways complementary.

9. Land fauna

(*a*) *Vertebrates*

Two mammals have been recorded, but the polar bear (*Thalarctos maritimus*) is only an occasional winter visitor. A number of arctic foxes (*Alopex lagopus*) were present. Ptarmigan (*Lagopus mutus hyperboreus*), one of the most usual summer foods of the arctic fox, were extremely scarce. One fox was seen capturing a puffin on the cliff edge, and probably much of their food was obtained from the sea-bird colonies. Most of the birds breeding by the fresh-water lakes nested on islets and so were inaccessible.

Apart from a few individuals of several species, none of which were proved to have bred in 1932 (**4**), the snow bunting (*Plectrophenax n. nivalis*) was the only Passerine bird. It was well distributed on the coast and inland where the rocks afforded crevices for nesting, but was absent from the upper parts of

Mount Misery, the Antarctic Mountains and almost the whole of the western part of the northern plateau, where the limestone did not afford crevices. Until the end of June, it fed mainly on vegetable matter, after this mainly on insects, capturing them on the wing on warmer days and searching for them among the boulders on colder ones. Another fruitful source was the snow patches, where numerous insects had fallen and remained in cold storage. Every available type of insect and spider of convenient size appeared to be taken. The only other land birds were a very few ptarmigan (*Lagopus mutus hyperboreus*), which feed on plants.

(*b*) *Arthropods*

The following table gives the typical habitat distributions of the commoner land Arthropods. (For complete list of species see Appendix 1.)

Table 1. *Characteristic habitat distribution of certain of the land Arthropods*

Group 1. *Under rocks, boulders and stones:*	
(N.B. The Trichoptera, Lepidoptera and Diptera were on the wing on warmer days.)	
Collembola	*Isotoma viridis*
Trichoptera	*Apatania arctica*
Lepidoptera	*Plutella maculipennis*
Diptera, Mycetophilidae 7 spp.	*Exechia frigida*
	Sciara spp.
Diptera, Chironomidae 26 spp.	*Procladius, Cricotopus, Spaniotoma, Chironomus, Tanytarsus,* etc.
Arachnida	*Coryphaeus holmgreni*
	Erigone tirolensis
Group 2 A. *In vegetation, moss and herb mat:*	
Collembola	See Table 2 and Appendix 1
Acarina	See Appendix 1
Group 2 B. *In herb mat (on the wing on warmer days):*	
Hymenoptera, Symphyta	*Amauronematus alberich*
	A. villosus
	Pristiphora frigida
Hymenoptera, Ichneumonidae	*Stenomacrus pedestris*
	Syndipnus beerensis
Diptera, Muscidae	*Limnophora megastoma*
Group 3. *On bird cliffs, under stones and in manured vegetation:*	
Collembola	*Achorutes viaticus*
Coleoptera, Staphylinidae	*Omalium septentrionis*
	Olophrum boreale
	Arpedium brachypterum
	(*Micralymma marinum* on cliff top but not in heavily manured areas)
Diptera, Mycetophilidae	*Boletina apicalis*
Diptera, Trichoceridae	*Trichocera lutea*
	T. maculipennis
Diptera, Cordyluridae	*Scatophaga nigripes*
Diptera, Helomyzidae	*Leria modesta*
	L. septentrionalis
Acarina	*Ameronothrus lineatus*

Note on Table 1

Table 1 is intended to give the typical distributions only. Thus all the animals in Group 1 occurred at times in the vegetation, and many of them on the less heavily manured parts of the bird cliffs. But since this has no special significance, except for *Isotoma viridis* and the larvae of

Mycetophilidae and *Plutella maculipennis* in vegetation, they are omitted from the other divisions. The species in group 2 B were occasional elsewhere. Group 3 is intended to include only those species of the bird cliffs which were much commoner here than elsewhere on the island. Many of the Collembola and Acarina, some of the Chironomidae and Mycetophilidae, and particularly the spider *Coryphaeus holmgreni* occurred in the less heavily manured parts, as they did over most of the island. But of these only the spider was present in as great numbers as elsewhere, though it was absent from the most heavily manured areas. Of the species in group 3 a number were occasional, and some regular, in other habitats, as discussed later.

Notes on the abundance of the different forms were not included in Table 1. But an idea of their relative abundance can be obtained from Appendix 1 in which various notes are given and, for most of the insects, the number of individuals collected.

Group 1. *Rock and boulder fauna.*

The winged insects in this group occurred under boulders on the sunless days, but since nearly all the days were sunless, they must be regarded as typical members of this habitat. The Chironomidae were sometimes extremely abundant, particularly near to the lakes. The spider *Coryphaeus holmgreni* was very widely distributed, often living even in the Steinflya, the central stony desert, where there was almost no vegetation. It was seen taking *Isotoma viridis* and also adult Chironomidae, and from the spider's presence in many places where Collembola and mites were scarce or absent, it is clear that its main food was adult Chironomidae on the days when the latter were sheltering under stones—a somewhat variable food supply.

Quite a number of the Chironomidae and Mycetophilidae (**6**), the spider *Erigone tirolensis* and the two cliff Staphylinidae, *Olophrum boreale* and *Arpedium brachypterum* (for the two last, see Fauna of bird cliffs) were curiously local in their distribution. For example, of 460 spiders collected, all were *Coryphaeus holmgreni* except ten. These ten *Erigone tirolensis* came from under stones in only two localities: Laksvatnet in the north, and Walrus Bay in the south, though there were many other places apparently similar to these; see also Bristowe (**5**).

Group 2 *A*. *Collembola and Acarina.*

The abundance of Collembola and Acarina was one of the most striking features of the Bear Island fauna. Presumably it is correlated with the relative abundance of mosses and lichens and the high humidity, in which respects Bear Island differed conspicuously from Hurry Inlet, East Greenland, where Collembola and Acarina were relatively much less common (**22**).

With the help of a Berlese funnel, the Collembolan fauna of 48 samples, which included all the main plant communities, was investigated, and the results are summarized in Table 2.

As can be seen from Table 2, most species of Collembola occurred in all the main habitats, except under bare stones, in the partially submerged Moss Bog and on the surface of the water. In general, the relatively dry Herb Mat supported very many fewer individuals than the damper Moss Heath and Moss Mat, Grass Mat (which was the dryest of all) being especially poor. But so far as the rather small number of samples enables one to judge, they were the

Table 2. *Distribution of the Collembola*

	Typical Herb Mat	Grass Mat	Moss Heath Moss Mat	Partially sub-merged Moss Bog	Tide line*	Glaucous gulls' nests	Bird cliffs	On water	Under stones
No. of samples	7	3	15	5	4	5	7	—	—
Onychiurus armatus	× ×	×	—	—	× × ×	× ×	×	—	—
Achorutes viaticus	×	×	× ×	× × ×	×	× ×	× × ×	—	—
Xenylla humicola	×	×	× ×	×	×	× ×	× ×	+	—
Tetracanthella wahlgreni	×	×	× ×	—	—	× ×	×	—	—
Folsomia quadrioculata	× × ×	×	× × ×	—	—	× ×	×	—	—
F. sexoculata	—	×	× ×	—	—	× ×	×	—	—
Isotoma viridis	×	×	×	—	×	×	×	—	+
Sminthurides malmgrenii	—	—	—	× ×	—	—	—	+	—

× indicates present in one-third or less of the samples examined, × × present in two-thirds or less, but more than one-third, and × × × present in more than two-thirds.

+ indicates recorded from this habitat, but no Berlese samples taken.

* The four samples on the tide line were at Evensenhamna, which was exceptionally rich in flotsam. Tide line samples from other parts of the island contained no life at all, except an occasional *Arpedium brachypterum* in the south.

same species in each of these habitats except that *Onychiurus armatus*, including var. *arcticus*, was not found in the closed Moss vegetation.

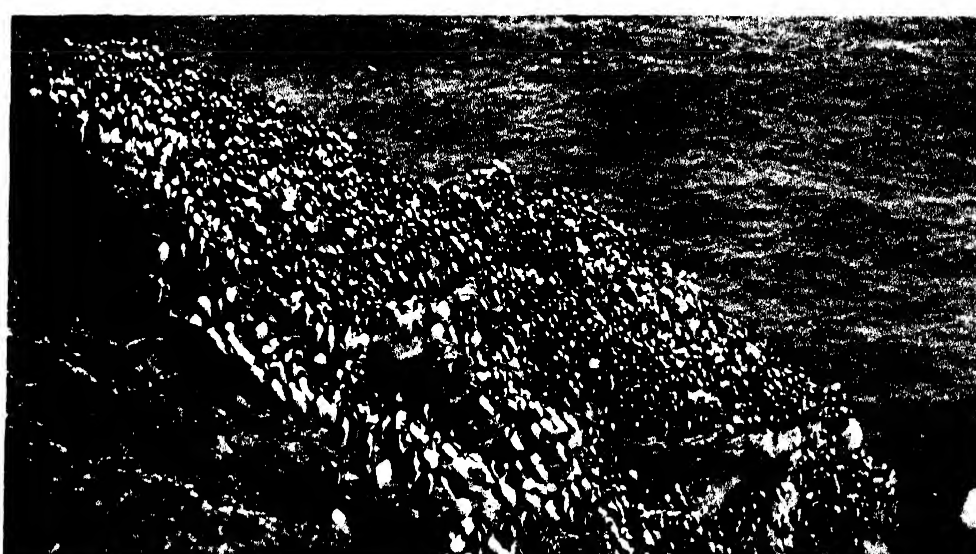
Mites were abundant wherever there were Collembola, particularly, like the Collembola, in closed Moss vegetation. Unfortunately, though hundreds of individuals were collected, too many species were apparently overlooked to make a table similar to that for the Collembola profitable. Thor (**30**) gives habitat notes on this group.

Group 2B. Winged insects of Herb Mat.

The two species of *Amauronematus* were widespread but never at all numerous. *Pristiphora frigida* was extremely local, being found only in Walrus Bay. The biology of these sawflies is unknown. One larva was found on *Salix polaris*, but died before pupating.

The two species of Ichneumonidae, and the fly *Limnophora megastoma*, emerged later in the summer and only on certain days, but were then extremely numerous; Roman (**10**) notes this as unusual for *Syndipnus*. Roman considers that *Syndipnus beerensis* probably parasitizes a sawfly and *Stenomacrus pedestris* a Mycetophilid fly. As adults these Ichneumonidae occurred chiefly in the flower heads. The latter were frequented when in season by many other Arthropods, including Chironomidae, most of the Diptera of the bird cliffs, the Staphylinid *Arpedium brachypterum* and also an occasional mite and Collembolan, all of which must therefore be included as temporary members of the Herb Mat.

Phot. 3. Grass mat, developed only on dry cliff tops near the nests of glaucous gulls (*Larus hyperboreus*) at Cape Dunér, West Coast.



Phot. 4. Small fraction of a guillemot (*Uria aalge* and *U. lomvia*) colony near the south end of the island.

Group 3. Fauna of the bird cliffs.

As before mentioned, only those species commoner on the bird cliffs than elsewhere are included in Group 3. Of these species, a few, such as *Omalium septentrionis* and the two species of *Leria*, were not found away from the bird cliffs (except that the two species of *Leria*, like other cliff forms such as *Boletina*, *Trichocera* and *Scatophaga*, at times visited the flower heads, particularly of *Sedum rhodiola* and *Saxifraga caespitosa*, on the cliff top). The other cliff Diptera were occasionally found some distance inland from the cliffs, but probably did not breed away from them. *Olophrum boreale* and *Arpedium brachypterum* each occurred sparsely in one inland and unmanured locality and the latter also on the tide line occasionally. *Achorutes viaticus* and *Ameronothrus lineatus*, though both frequent inland, were astoundingly abundant on the bird cliffs. Summerhayes & Elton (**28**, **29**), Madsen (**24**) and Jørgensen (**21**) record these two last, from coastal and/or manured areas.

Scatophaga and *Leria* are characteristic of manured habitats elsewhere, like *Cochlearia* among the plants. But the occurrence of the *Omalium*, *Olophrum*, *Arpedium* and *Trichocera* in manured areas on Bear Island seems analogous to that of the Grass Mat. Typically they are much more generally distributed, but on Bear Island conditions are presumably too severe except on the bird cliffs. It is of interest that *Olophrum boreale* and *Arpedium brachypterum* each occurred in one inland locality (the former by Laksvatnet and the latter at the north foot of Mount Misery) and that the specimens of the former were markedly smaller than those from the bird cliffs. The three species of Staphylinidae appeared to feed mainly on decaying matter (**7**), and their restriction to the bird cliffs may have been directly correlated through food supply with the general scarcity of decaying matter on the normal terrain of the high Arctic.

Micralymma marinum occurred only under stones in certain dry localities on the cliff top which received a small amount of manuring. It was not found inland or on the heavily manured bird cliffs.

As regards the fauna of manured areas away from the bird cliffs, in Grass Mat the Collembola and mites were similar to those of typical Herb Mat, but the individual total was very much smaller. Hymenoptera and *Limnophora megastoma* were absent from Grass Mat. Thus Grass Mat has much the poorest fauna of any vegetation on the island. The manured closed moss vegetation was similar to unmanured, except that round some of the most manured lake margins *Achorutes viaticus* was extremely abundant.

Fauna of birds' nests.

The Arthropods in all the main types of birds' nests were examined. In all cases except two, details have been omitted here since the animals were those typical of the materials of which the nest was composed or of the surrounding vegetation, and hence birds' nests do not greatly affect the Arthropod fauna. (The Collembola from glaucous gulls' nests are recorded in Table 2.) But one

eider's nest, out of many examined, contained five specimens of *Microprosopa frigida* (**6**), a species of Cordylurid Diptera which was not collected elsewhere. The one nest of a snow bunting examined contained a single *Enicmus minutus* and four large black Sminthurid springtails, probably *Sminthurinus niger*. (The nests of other species examined included starling, long-tailed duck, purple sandpiper, red-throated and great northern divers, arctic tern, arctic skua and kittiwake.)

(*c*) *Animal communities*

The above tabulation into four main habitats seems the most satisfactory for the Bear Island Arthropoda. Summerhayes & Elton (**28**) list the animals found in each plant community, but, as they remark, though each plant community has a fairly constant set of animal species associated with it, few of these animals are exclusive. This the 1932 survey bears out, and it arises because the plant communities as defined by the botanist are by no means necessarily significant as regards the factors limiting the animals. Hence the classification of the animal distributions in terms of such communities seems of doubtful value. A similar conclusion has been reached by Jørgensen (**21**) who, working on the Collembola and Acarina of East Greenland collected from many types of plant associations, classifies them into four communities based primarily on the degree of humidity. A classification based on the lower plants, on which the Collembola and mites depend, might be significant, for the lower plants also depend on the humidity, but not one based directly on the higher plants.

(*d*) *Temperature effects*

That the average air temperature for July, the hottest month, is only 4·2° C. has an important effect on the flying insects. Thus, although Chironomidae were extremely abundant, aerial swarms were seen only on a few of the warmest days. For the rest of the time, the Chironomidae were found chiefly under the boulders. It seems primarily because of this fact that the spider *Coryphaeus holmgreni* can be so widespread. The caddis, *Apatania arctica*, and the Mycetophilidae were also under the boulders on the less warm days.

The sawflies emerged in June and were active at lower temperatures than the other species of the Herb Mat. The two species of Ichneumonidae, and the fly *Limnophora megastoma* emerged only in July onwards and were active on extremely few days. In particular *Stenomacrus pedestris* was first recorded on 23 July, and was numerous on only 3 days between then and 10 August, a few individuals being out on 3 other days. Experiments could not be carried out on the lines adopted by Bertram (**12**) in Greenland in 1933, but from observation it seems probable that the two Ichneumons and *Limnophora megastoma* required an air temperature of at least 6° C. before they appeared. In the periods between the warm days, they retired into the Herb Mat; on one occasion they were seen appearing in swarms from a patch of *Salix polaris*

when the temperature rose. Presumably the number of sunny days in late summer on Bear Island very materially affects the number of matings which take place and of eggs laid.

As in the lakes the temperature in the vegetation and to a less marked extent under the boulders was usually higher than that of the air. Temperatures in the micro-habitats were measured roughly, with an ordinary Centigrade thermometer, no more precise means being available for systematic observations. In general it was found that on the typical foggy days with an air temperature of 3–5° C. the temperature in the vegetation was at least 2 or 3 degrees higher. This may perhaps be important for the Collembola and mites though the critical temperature for activity in the Bear Island forms is not known. It may also be noted that when the winged Diptera and Ichneumonidae retired, according to their kind, under boulders or into the vegetation, they moved into areas of more suitable temperature.

In most cases the temperatures in the micro-habitats on the manured bird cliffs were not significantly higher than those elsewhere. A marked exception was the moss nest of a glaucous gull, built on the remains of at least six previous nests, the whole structure being 50 in. in diameter and 18 in. deep. In this the temperature near the centre was 24·5° C., much the highest temperature recorded on Bear Island. The nest contained many Dipterous larvae (chiefly of *Leria*) and the increased temperature presumably accelerated their rate of development. But large nests of this type were rare, and so far as our rough measurements showed, decaying matter was not normally important in raising the temperature of the cliff micro-habitats.

PART 3. SOME GENERAL ASPECTS

10. Composition of the fauna

A full list of the known Bear Island Vertebrates and Arthropods is given in Appendix 1. As compared with the Palaearctic land mass to the south, Bear Island has far fewer species in every group. The fauna is also poorer than that of the warmer parts of Spitsbergen, but is much richer than, for instance, North East Land (**29**).

Among the Arthropods, notable absentees as compared with the Spitsbergen list are Neuroptera, Hemiptera, Curculionidae, Empidae, Syrphidae, Culicidae and large Lepidoptera. Further only five species of parasitic Hymenoptera have been recorded from Bear Island, but some ten other species from Spitsbergen. Two species of spiders occur on Bear Island, these and some nine others in Spitsbergen. Fifteen species of fresh-water Crustacea occur on Bear Island, 11 of these and 15 others in Spitsbergen. There is a similar paucity of Diptera on Bear Island as compared with Spitsbergen. In the great majority of cases the species in these groups which occur in Spitsbergen, but not on Bear Island, occur on the Palaearctic land mass to the south, and in Spitsbergen

are confined to the warmer parts, especially near the heads of the fjords. Presumably a climatic factor, probably temperature, is concerned in their absence from Bear Island.

These facts accord with the botanical data on which Summerhayes & Elton (**29**) put Bear Island in the most barren of the four floral zones into which they divided Spitsbergen. On the other hand, they noted certain resemblances to the more favourable zones 3 and 4, and this is borne out by the presence on Bear Island of the spiders *Coryphaeus holmgreni* and *Erigone tirolensis*, the sawflies *Pristiphora frigida* and *Amauronematus villosus*, the caddis *Apatania arctica* and the moth *Plutella*, which are recorded from Spitsbergen only in the warmer zones. (The *Plutella* is a different species.) Further a few species, notably all five species of Coleoptera, eight of Diptera (*Procladius crassinervis, Spaniotoma oxonianus, Chironomus psilopterus, Tanytarsus gracilentus, Cynomyia mortuorum, Leria modesta, Leria septentrionalis* and *Piophila vulgaris*), four of fresh-water Crustacea (*Daphnia longispina, Sida crystallina, Cyclops gigas* and *Cyclops viridis*), and the water mite *Sperchon lineatus*, are known from the Palaearctic land mass and Bear Island, but not from Spitsbergen. In certain cases (probably in most of the Diptera) the apparent absence of these from Spitsbergen is almost certainly due to lack of collecting, but some at least probably represent a small more southern element in the Bear Island fauna.

It is curious that the five species of Coleoptera found on Bear Island have not been recorded from Spitsbergen and that the four species known from Spitsbergen have not been found on Bear Island.

Of the Arthropoda common to Bear Island and Spitsbergen, nearly all the Collembola and mites, at least ten species of Diptera, both species of spider and the caddis *Apatania arctica* occur also in Greenland, and may be regarded as widely distributed Arctic forms. Three species of Diptera, the most interesting being *Simulium ursinum*, have been recorded from Bear Island and Greenland but not Spitsbergen. Apart from four species of Diptera, all of which Dr Edwards considers to be of doubtful validity, the sawfly *Amauronematus alberich* is the only species recorded only from Bear Island, and this last case may well be due to lack of collecting elsewhere.

Coming to Vertebrates, the one fish, the arctic char, is a widely distributed species. Of the mammals, both arctic fox and polar bear are circumpolar. Spitsbergen possesses these, and also the reindeer, absent from Bear Island. Of the 26 species of birds breeding (including doubtfully breeding) on Bear Island, 17 are common to Spitsbergen and the Palaearctic land mass. Six, namely herring gull, razorbill, common guillemot, and, of doubtful breeding species, starling, tufted duck and golden plover, breed in Norway and Bear Island, but not Spitsbergen. Two only, the grey phalarope and little auk, both circumpolar species, breed in Spitsbergen and Bear Island but not on the Palaearctic land mass. On the other hand, eight species typical of the most

northerly parts of the Arctic breed in Spitsbergen but not on Bear Island: pink-footed, barnacle and brent geese, king eider, knot, sanderling, Sabine's and ivory gulls. (In addition several other more widely distributed species breed in Spitsbergen and not on Bear Island.) One species, the great northern diver which breeds on Bear Island, also in Iceland, Greenland and Arctic America, has not as yet been recorded breeding either in Spitsbergen or Scandinavia, but may perhaps breed in the latter places as it has been observed there during the summer.

Hence the birds of Bear Island are definitely more southern in character than those of Spitsbergen, in marked contrast with the Arthropods, in which Spitsbergen, not Bear Island, possesses a larger southern element. This contrast results mainly from two differences between these groups of animals. First, Arthropods are poikilothermous, birds homoiothermous. The warmer temperatures of parts of Spitsbergen as compared with Bear Island will tend to maintain more southern type of Arthropod fauna in Spitsbergen than on Bear Island, although Spitsbergen is farther north. Birds, being homoiothermous, are relatively less dependent on temperature. Secondly, Arthropods are distributed geographically largely by chance, whereas most birds have a well-developed habit of returning to where they bred or were hatched the year before, and have great powers of flight which normally insure that this takes place.

There is probably not much difference between the relative chances of an air-born Arthropod reaching Bear Island or Spitsbergen. Many birds, on the other hand, could reach either with ease, but have a controlled dispersal and tend to colonize the areas nearest to their ancestral home before those further away; hence there is a stronger southern element in the Bear Island than the Spitsbergen avifauna, correlated with the more southerly geographical position of Bear Island, and in spite of the superior climate of much of Spitsbergen.

To sum up, the Arthropod fauna colonizes by passive chance dispersal and survives wherever conditions are sufficiently good. On the other hand, the dispersal of birds is a more active process and they tend to colonize first those areas nearest the original home.

11. Origins of the fauna

That there has been no post-glacial land bridge between Bear Island and the Palaearctic land mass can scarcely be doubted. Therefore the animals now on Bear Island have either survived from pre-glacial times or colonized since by crossing a wide stretch of sea.

It has frequently been assumed that no life could have existed in Svalbard during a glaciation. If the whole land was covered completely with snow and ice, this was presumably the case, but it seems possible that there was a narrow coastal belt or projecting nunataks or both, free of snow at least during part of the summer. To test whether any animal life could exist in such

conditions the two writers, with B. B. Roberts, investigated the fauna of a nunatak above 3000 ft. at the head of the Emmanuel Glacier, in Liverpool Land, East Greenland, in 1933 (**22**). Under what must be the most severe conditions of ice-free land in the Arctic, a fauna of three species of Collembola, and the larvae of a Chironomid fly (also a single pullus of an Erigonine spider, perhaps not a permanent member of the fauna) were found. Hence these forms at least, and probably also various kinds of mites (see Thor, **30**) might be capable of surviving a glaciation if ice-free land existed. Bear Island is low, and nunataks could scarcely have existed, but the possibility must be borne in mind that certain forms survived on a coastal belt and colonized Bear Island from there.

Thor (**30**) considers that the mites and Collembola of Svalbard represent a pre-glacial element, and adduces three main reasons. First, such forms are extremely resistant to low temperature and could probably have survived, given ice-free land. This we agree in considering possible. Secondly, the members of these groups found in Svalbard are members of the most primitive and least specialized families (with the exception of *Sperchon lineatus*, confined within Svalbard to Bear Island, which Thor considers quite possibly has colonized in post-glacial times). From this Thor argues that these forms, but not the more specialized families, were on Bear Island in pre-glacial times, and that the absence of the specialized forms to-day is due to the absence of post-glacial colonization. This is a doubtful argument, for perhaps both primitive and specialized types may have had opportunity for post-glacial colonization, but only the primitive have found the conditions sufficiently good for survival. Thor also states that it is often the Scandinavian mountain forms, not the coastal ones, which occur on Bear Island, whereas he would have expected the coastal ones to have had better chances of post-glacial dispersal. This also may depend on the relative suitability of the conditions.

Thirdly, Thor states that the postulated means of post-glacial colonization, through drift ice, drift wood, ships, birds and the air, are extremely doubtful for such wingless forms, and certainly cannot account for their wide distribution in Spitsbergen in many fjords and bays which are separated from each other by ice and sea. Such erratic dispersal, so he considers, would result in erratic distributions. With this we agree so far as the first four means of dispersal are concerned, but aerial dispersal cannot now be ruled out so easily, for collections made from heights up to 14,000 ft. by aeroplanes (Coad, **14**), show clearly that mites, Collembola and spiders are not uncommon high in the air. Hence these forms would have had little difficulty in reaching Svalbard post-glacially, though whether in sufficient numbers to account for their present wide distributions is perhaps more doubtful.

The rest of the Bear Island Arthropods and Vertebrates most certainly could not have survived a glaciation, and we believe that all could have colonized in post-glacial times aerially, except for the arctic fox and polar bear

which regularly cross on the ice in winter. Further, as compared with the Palaearctic land mass and with Greenland, those mammals that cannot cross on the ice (lemming, ermine, arctic hare, musk ox) are absent from Svalbard, as are also Lycosid spiders, which is evidence for the absence of a post-glacial land bridge. Elton (**18**, **19**) strongly advocates this view, and also provides data on a remarkable dispersal of insects to Spitsbergen, though Thor (**30**) thinks it conceivable that these were of local origin, which is profoundly unlikely.

If most of the Bear Island fauna has colonized in post-glacial times, there is no reason to suppose such colonization to have finished. In only two groups, the birds and the fresh-water Crustacea, are there adequate comparisons with the past. Among the birds (**4**) there is clear evidence that herring and great black-backed gulls have established themselves only recently, and other more southern species appear to be attempting to establish themselves. Among the Crustacea, Bertram (**2**) has shown good evidence for thinking *Daphnia pulex* to have colonized only of late years, for though previously unrecorded, in 1932 it was widely distributed, being specially common in one lake visited by all previous collectors.

To sum up, all of the Bear Island fauna would have had little difficulty in colonizing in post-glacial times in the absence of a land bridge, and at least among the birds and Crustacea colonization is still continuing. Most forms could not have survived a glaciation, but it is possible that certain Collembola, mites and Chironomid flies represent a pre-glacial element, though they may equally have colonized since.

12. NOTES ON POPULATION CONTROL

Observations on the limits to population density in natural populations are still extremely scanty. Within the space of one summer the writers obviously could not contribute anything very definite to this problem, but some remarks (which must be regarded as extremely tentative) on the rather peculiar conditions of Bear Island may not be out of place.

In general the Arctic as compared with Temperate regions possesses few species but many of these are extremely abundant. Bear Island exhibits both tendencies to an extremely marked degree. The paucity of species is obvious from Appendix 1. The major factor involved is probably the severity of the climate, acting both directly and indirectly through the consequent sparseness of the plant life. But it has certainly been assisted by the isolated position of the island; animals which would find Bear Island suitable have not yet colonized. Indeed colonization is still continuing. As a result, Bear Island cannot be considered ecologically "full". Many niches, particularly of larger predators, are empty. For example the bird cliffs would support Accipitrine birds of prey, and the Chironomidae would support many more insectivorous birds.

Though quite a number of species were local or rare, others were extremely

abundant, as illustrated by the large numbers collected. As instances of exceptional abundance, the following may be cited. On one occasion on the mud by a manured lake there was a *continuous* black carpet some 10 yd. long and 1 or 2 yd. broad consisting of a swarm, in many places two to four individuals deep, of *Achorutes viaticus* (each of which is only 2 mm. long). Again on certain days round several of the lakes there was a grey sludge which could be picked up in bucketfulls, this mass consisting entirely of the cast skins of Chironomidae which had drifted ashore. Ichneumonidae are usually met singly or in small numbers, but on the days when the two Bear Island species appeared, they occurred in hundreds. Finally the colonies of sea birds, particularly of common and Brünnich's guillemots in the south, are said to be the largest in the northern hemisphere; their numbers have to be seen to be believed, and certainly even the most crowded British colonies leave one quite unprepared for the spectacle (Pl. 4, phot. 4).

The guillemots are of interest as regards the limit to their density. Almost certainly on so isolated an island their marine food supply is normally far in excess of their needs. Apart from glaucous gulls, which take some of their eggs and young, they normally have no predators. The birds nest on flat ledges, chiefly on the cliff faces, but also over the flat tops of stacks and islets and also on flat areas above the cliffs on the main island where these are separated from the top by further cliffs. But any expansion on to the flat top of the main island would render the birds at once accessible to arctic foxes. Hence the arctic foxes, though normally inoperative as predators, yet may set an effective upper limit to density, i.e. that at which every inaccessible nesting site is fully occupied.

Similar considerations probably apply on Bear Island to the eider ducks, the great majority of which nested on the lake islets, where the nests are extremely numerous. Apart from a few glaucous gulls and arctic skuas which took eggs if the owner was absent, the eider normally had no predators, but though a few pairs bred successfully on the main land, arctic foxes prevent this on a large scale. An arctic fox was seen trying to cross to one of these islets, but gave up on reaching the furthest boulder projecting above the water. (It may be noted that although 1932 was a very late year, no eiders began to nest on the lake islets until the surrounding ice (and the consequent connexion with the main land) had disappeared, Lack (**9**)).

Hence predators limited the number of breeding eiders very materially, as inaccessible lake islets were few. Further, overcrowding on the islets probably reduces the number of offspring reared. Of this a definite example was found; in two nests very close together the one female took under her the clutch of her neighbour who then deserted. (As is well known a number of birds fetch eggs placed outside into their own nest.) The clutches were laid at different times, and the female went off with the first brood to hatch, thus leaving the other clutch of five eggs to die.

Apart from the above birds, where the effect of predators is correlated with overcrowding of breeding grounds, few Arthropods or Vertebrates on Bear Island seemed seriously affected by predators. The ptarmigan, eaten by the arctic fox, are exceptions, and the Mycetophilid and the sawfly parasitized by the Ichneumons may be others. Other cases probably occur, but for the three most prominent groups of land Arthropods, predators seem of little importance. For example, the only important predator of the Collembola was the spider *Coryphaeus holmgreni*, while snow bunting and purple sandpiper probably took a few, but Collembola were abundant in many places where these predators were rare or absent. Similar considerations applied to the Acarina. The Chironomidae were preyed on as larvae by the arctic char, which certainly took a great many to judge from stomach contents, but this fish was absent from many of the smaller ponds where Chironomidae were abundant. Chironomidae were also preyed on as larvae and adults by the arctic tern, but these birds, breeding mainly on lake islets, were extremely local. Adults formed a large part of the diet of the snow bunting, but this bird was scarce and local, in particular being absent from almost the whole of the western part of the northern plateau where nesting crevices were absent. Purple sandpiper, grey phalarope and other birds preyed on them, but all were scarce and local. *C. holmgreni* took them when they were under stones on the colder days, but the Chironomidae were extremely numerous in many places where the spider was absent. Hence although Chironomidae were the basis of the diet of a number of forms, over the greater part of their range the total of predators could in our opinion have had only a negligible effect on their huge numbers. The same applies even more markedly to the Collembola and Acarina, and perhaps helps to explain the enormous numbers of these three groups on Bear Island.

Evidence for animals limited in density by food on Bear Island is small, but is very hard to obtain. The larvae of *Simulium ursinum*, restricted to those streams which drained lakes rich in plankton, may be a case in point, and the arctic fox may be another. But the rate of increase of at least a number of Arctic species cannot be regarded as at all constant, the variation from year to year being due to climatic effects. Two examples were prominent on Bear Island. In 1932 a large number of adult birds (75% or more in some species) failed to breed, and it has been shown (**13**) that this extensive non-breeding occurs frequently in the high Arctic, correlated fundamentally, it is believed, with some climatic factor. Secondly, the number of days on which the air temperature was sufficiently high for the activity of certain winged insects, notably *Stenomacrus pedestris*, was extremely small, and even one sunny day more or less might greatly affect the number of matings in a given year, and the size of the next generation.

Food supply obviously can set an upper limit to the density of population of any animal on Bear Island, and perhaps the populations of many of the

animals are so limited. But the Arctic differs from temperate regions both in the severity of its climate and in the much smaller number of species, particularly of predators and parasites, in the animal communities. It seems possible that the severe and markedly fluctuating climate, affecting both mortality and fecundity, may so greatly modify the usual predator-prey relationships **(25)** that in places such as Bear Island these may lose much of their normal importance. But until our knowledge is more abundant and precise these are mere hypotheses.

13. Summary

1. The island, its climate and flora are briefly described, and then follows an account of the Vertebrate and Arthropod faunas of the various habitats.

2. Summer temperatures are normally low, but even on the typical foggy days the temperature of the lakes and among plants was several degrees higher than that of the air. Certain winged insects were active in the air only on the extremely few warm days.

3. The humidity is extremely high in summer, contributing to an abundance of mosses and lichens, and of Collembola and Acarina.

4. A characteristic flora and fauna are found on the bird cliffs, some of its members being typical of such habitats farther south and others being typically more widely distributed, but confined to this habitat on Bear Island owing to the severity of the conditions over the general terrain.

5. The land animals were classified in four main groups, the plant communities not being used for this purpose as they often do not correspond with the factors affecting the animals.

6. The Arthropod fauna of Bear Island is more northern in character than that of the inner fjord regions of Spitsbergen, but contains a few southern elements not found in the latter. The avifauna is definitely more southern in character than that of Spitsbergen. The reasons for this contrast are discussed.

7. There has been no land bridge with Bear Island after the glaciation. All of the fauna could have colonized post-glacially, aerially or on the ice, and colonization is still continuing. Most forms could not have survived a glaciation, but certain species may represent a pre-glacial element, though equally they may have colonized since.

8. Though species are few, the individual total is in some cases extremely large, spectacular examples of which are given.

9. The arctic fox, normally inoperative as a predator, may set an effective upper limit, correlated with a limited number of inaccessible nesting sites, to the numbers of guillemots and eiders.

10. It is tentatively suggested that a severe and fluctuating climate, affecting both mortality and fecundity, may greatly modify the predator-prey relationships which have been postulated on theoretical grounds, and which are perhaps typical of temperate regions with a less severe climate and a much greater number of species.

REFERENCES

A. RESULTS OF THE 1932 EXPEDITION TO BEAR ISLAND

1. **Benson, R. B.** (1934). "Sawflies from Bear Island." Ann. Mag. Nat. Hist. 14: 207–13.
2. **Bertram, G. C. L.** (1933). "The freshwater Crustacea of Bear Island." Ann. Mag. Nat. Hist. 12: 538–43.
3. **Bertram, G. C. L. & Lack, D.** (1933). "Bear Island." Geogr. J. 81: 45–53.
4. **Bertram, G. C. L. & Lack, D.** (1933). "Notes on the birds of Bear Island." Ibis, pp. 283–301.
5. **Bristowe, W. S.** (1933). "The spiders of Bear Island." Norsk Entom. Tids. 3: 149–54.
6. **Edwards, F. W.** (1935). "Diptera from Bear Island." Ann. Mag. Nat. Hist. 15: 531–43.
7. **Lack, D.** (1933). "Trichoptera, Lepidoptera, and Coleoptera from Bear Island." Ann. Mag. Nat. Hist. 12: 205–10.
8. **Lack, D.** (1932). "The birds of Bear Island." Bull. Brit. Orn. Club. 53: 64–9.
9. **Lack, D.** (1933). "Nesting conditions as a factor controlling breeding time in birds." Proc. Zool. Soc. Lond.: pp. 231–7.
10. **Roman, A.** (1934). "Parasitic Hymenoptera from Bear Island." Ann. Mag. Nat. Hist. 14: 203–7.

B. OTHER REFERENCES

11. **Anderson, F. W. & Falk, P.** (1935). "Observations on the ecology of the central desert of Iceland." J. Ecol. 23: 406–21.
12. **Bertram, G. C. L.** (1935). "The low temperature limit of activity of Arctic insects." J. Anim. Ecol. 4: 35–42.
13. **Bertram, G. C. L., Lack, D. & Roberts, B. B.** (1934). "Notes on East Greenland birds, with a discussion of the periodic non-breeding among Arctic birds." Ibis, pp. 816–31.
14. **Coad, R. C.** (1931). Yearbook of Agriculture (publ. U.S. Dept. Agric.), p. 320.
15. **Coward, T. A.** (1929). "The birds of the British Isles and their eggs." 2: 68.
16. **Dahl, K.** (1926). "Contributions to the biology of the Spitsbergen char." Skrifter om Svalbard og Ishavet, No. 7.
17. **Davis, D. H. S.** (1936). "A reconnaissance of the fauna of Akpatok Island, Ungava Bay." J. Anim. Ecol. 5: 319–32.
18. **Elton, C.** (1925). "The dispersal of insects to Spitsbergen." Trans. Ent. Soc. Lond. pp. 289–99.
19. **Elton, C.** (1929). "Aphids and hover-flies in North-East Land (Spitsbergen) in 1924: an additional note." Proc. Ent. Soc. Lond. 4: 76–7.
20. **Horn, G. & Orvin, A. K.** (1928). "Geology of Bear Island." Skrifter om Svalbard og Ishavet, No. 15.
21. **Jørgensen, M.** (1934). "A quantitative investigation of the microfauna communities of the soil in East Greenland (preliminary report)." Medd. Grønl. 100, No. 9.
22. **Lack, D.** (1934). "Some insects from the Scoresby Sound region, East Greenland, with an account of the fauna of a nunatak." Ann. Mag. Nat. Hist. 14: 599–606.
23. **Longstaff, T. G.** (1932). "An ecological reconnaissance in West Greenland." J. Anim. Ecol. 1: 119–42.
24. **Madsen, H.** (1936). "Investigations on the shore fauna of East Greenland with a survey of the shores of other arctic regions." Medd. Grønl. 100, No. 8, pp. 1–79.
25. **Nicholson, A. J.** (1933). "The balance of animal populations." J. Anim. Ecol. 2: 132–78.
26. **Resvoll-Holmsen, H.** (1927). Svalbards Flora.
27. **Scholander, P. F.** (1934). "Vascular plants from Northern Svalbard." Skrifter om Svalbard og Ishavet, No. 62.
28. **Summerhayes, V. S. & Elton, C. S.** (1923). "Contributions to the ecology of Spitsbergen and Bear Island." J. Ecol. 11: 214–86.
29. **Summerhayes, V. S. & Elton, C. S.** (1928). "Further contributions to the ecology of Spitsbergen." J. Ecol. 16: 193–268.
30. **Thor, S.** (1930). "Beiträge zur Kenntnis der Invertebraten Fauna von Svalbard." Skrifter om Svalbard og Ishavet, No. 27.

APPENDIX 1

Complete list of vertebrates and arthropods from Bear Island

(*Note.* As an indication of abundance, notes are given after each species. In the case of the birds, the number denotes the number of pairs as estimated by an approximate census. In the insects and spiders, the number indicates the number of individuals collected by us, which gives a *rough measure* of relative frequency. Species marked * were not recorded by us.)

MAMMALS.

Alopex lagopus	Arctic fox	About 12
**Thalarctos maritimus*	Polar bear	None in summer, 1932, two in winter 1931–32

BIRDS. (Only breeding and possibly breeding species are included; for full list see Bertram & Lack (**4**).)

Sturnus vulgaris L. (doubtful)	Starling	1
Plectrophenax n. nivalis (L.)	Snow bunting	100
Nyroca fuligula (L.) (doubtful)	Tufted duck	1
Clangula hyemalis (L.)	Long-tailed duck	70
Somateria mollissima borealis (Brehm)	Northern eider	1000
Melanitta nigra (L.)	Common scoter	15
Fulmarus g. glacialis (L.)	Fulmar	Very many
Colymbus immer Brünn.	Great northern diver	2
C. stellatus Pont.	Red-throated diver	80
Charadrius hiaticula L. (doubtful)	*Ringed plover	None in 1932
C. apricarius altifrons Brehm (doubtful)	*Golden plover	None in 1932
Calidris m. maritima (Brünn.)	Purple sandpiper	200
Phalaropus fulicarius jourdaini Iredale	Grey phalarope	12
Sterna macrura Naumann	Arctic tern	250
Larus a. argentatus Pont.	Herring gull	7
L. marinus L.	Great black-backed gull	35
L. hyperboreus Gunn.	Glaucous gull	8000
Rissa t. tridactyla (L.)	Kittiwake	Many
Stercorarius parasiticus (L.)	Arctic skua	175
Alca torda L.	Razorbill	6
Uria aalge hyperborea Salomonsen	Common guillemot	Very very many
U. l. lomvia (L.)	Brünnich's guillemot	Very very many
U. grylle mandtii Mandt	Mandt's guillemot	Fair numbers
Alle a. alle (L.)	Little auk	Very many
Fratercula a. arctica L.	Norwegian puffin	Many
Lagopus mutus hyperboreus Sund	Spitsbergen ptarmigan	3

FISH.

Salvelinus alpinus	Arctic char	Fairly common

INSECTA.

Collembola. (All species recorded by us were numerous except for the two species of Sminthuridae which were scarce.)

Onychiurus armatus (Tullb.) including var. *arcticus* (Tullb.)
Achorutes viaticus (Tullb.)
Xenylla humicola Fab.
Tetracanthella wahlgreni (Axels.)
**Agrenia bidenticulata* (Tullb.)
**Folsomia binoculata* (Wahlgren)
F. quadrioculata (Tullb.)
F. sexoculata (Tullb.)
Isotoma viridis Bourl.
**I. violacea* Tullb.
**I. multisetis* Carp. & Phil.
Smithurides malmgrenii (Tullb.)
Smithurinus niger (Lubb.)
**S. aereus* (Lubb.)

Trichoptera

Apatania arctica Bohem.	Common

Lepidoptera

Plutella maculipennis Curt.	2

Coleoptera

Micralymma marinum Stroem.	30
Omalium septentrionis Th.	44
Olophrum boreale Payk.	29
Arpedium brachypterum Er.	26
Enicmus minutus L.	2

Hymenoptera

Amauronematus alberich Benson	12
A. villosus Thoms.	11
Pristiphora frigida Bohem.	16
**Microcryptus erraticus* Holmgr.	
**Aclastus gracilis minutus* Bridg.	
Stenomacrus pedestris Holmgr.	82
Syndipnus beerensis Roman	78
**Biosteres* sp.	

Diptera

Boletina apicalis (Walk.)	45
Exechia frigida Holmgr.	50
Sciara tridentata Rubs.	10

INSECTA (*cont.*)

DIPTERA (*cont.*)

Sciara holmgreni Rubs.	2
Sciara sp. indet.	1
S. consimilis Holmgr.	16
S. parva Holmgr.	10
**S. röderi* Lengersdorf	
Simulium ursinum Edwards	Many larvae, 9 pupae
Pentaneura barbitarsis (Zett.)	4
Procladius crassinervis (Zett.)	40
Diamesa septima Edw.	4
**D. hyperborea* Holmgr.	
**D. ursus* Kieff	
Metriocnemus obscuripes Holmgr.	10
M. ursinus Holmgr.	5
Cricotopus basalis Staeg.	20
Spaniotoma limbatellus Holmgr.	20
S. subpilosus Kieff	17
S. consobrinus (Holmgr.)	Numerous
S. decoratus (Holmgr.)	4
S. mixtus (Holmgr.)	2
**S. festivus* Holmgr.	
**S. petraeus* var. *ursinus* Kieff.	
S. eltoni Edw.	8
S. longicosta (Edw.)	2
Spaniotoma sp. inc.	5
**S. flexinervis* Kieff (? *longicosta* Edw.)	
**S. oxonianus* Edw.	
Chironomus hyperboreus Staeg.	18
C. lugubris Zett.	6
C. psilopterus Edw.	25
Tanytarsus gracilentus Holmgr.	100
T. praecox Goet.	17
T. mimulus (Holmgr.)	60
Trichocera lutea Becher	19
T. maculipennis Mg.	29
Cynomyia mortuorum L.	1
Limnophora megastoma (Bohem.)	61
Scatophaga nigripes Holmgr.	31
Microprosopa frigida (Holmgr.)	5
Leria modesta Mg.	48
L. septentrionalis Collin	39
Piophila sp., cf. *vulgaris* Fln.	1

CRUSTACEA

BRANCHIOPODA

Lepidurus arcticus (Pallas)	Widely distributed
Sida crystallina (Müller)	1 lake
Daphnia pulex (De Geer)	Fairly frequent
D. longispina (Müller)	2 lakes
Macrothrix arctica Sars	6 lakes
Acroperus harpae Baird	1 lake
Chydorus sphaericus Müller	Well distributed

COPEPODA

Cyclops strenuus Fischer	Widely distributed
C. gigas Claus	Well distributed
**C. viridis* (Jurine)	
C. crassicaudis Sars	1 lake
C. vicinus Uljanin	5 lakes
**Maroenobiotus brucei* (Richard)	

OSTRACODA

Eucypris glacialis (Sars)	1 lake
Candona candida Müller	1 lake

ARACHNIDA

ARANEIDA[1]

Coryphaeus holmgreni Thor.	450
Erigone tirolensis Koch	10

ACARINA.

Note. The following list and comments are taken from Thor (**30**), except that *Biscirus lapidarius* and *Molgus littoralis* were recorded by us and not Thor. (Thor recorded them from Spitsbergen.) Dr Finnegan wrote that our collection contained eleven species, namely those without asterisks in the following list and also *Hermannia* n.sp., *Pergamasus* sp. deutonymph, *Nothrus* n.sp. and *Eupodes* sp.

**Nothrus horridus* (Hermann)	Very common
**Hermannia reticulata* Thorell	Very common
Ameronothrus lineatus (Thorell)	Rather scarce (Thor) extremely abundant (Bertram & Lack)
**Oribata ursina* Thor	One example
**Dameosome ornatum* (Oudemans)	3 examples
Ceratoppia hoeli Thor (*Notaspis bipilis* var. *sphaerica* (L. Koch))	Not uncommon
**Oribatula exilis* (Nic.)	Fairly common
Murcia notata (Thorell)	Extremely common
**Calyptozetes sarekensis* (*Tragardh*)	Common locally
**Tydeus foliorum* (*Schrank*)	Fairly common
**Eupodes variegatus* Koch	Occasional
**E. clavifrons* Canestrini	Fairly common
**Penthalodes ovalis* (Dugès)	Common
**P. maior* (Dugès)	Not common
Rhagidia gelida Thorell	Fairly common
**Alycus arboriger* Berlese	Fairly common
**Cyta latirostris* (Hermann)	Widespread
Biscirus lapidarius (Kramer)	(Recorded by us not Thor)
**Molgus capillatus* (Kramer)	Common
M. littoralis (Linn.)	(Recorded by us not Thor)
Sperchon lineatus Thor	Local
**Zercon triangularis* Koch	3 examples

[1] The numbers given for the spiders are not directly to be compared with those for the insects.

APPENDIX 2

Acknowledgements

The expedition of which this paper is a result would never have been possible without assistance from many quarters. We must particularly record our gratitude to the Royal Geographical Society and to Magdalene and St John's Colleges, Cambridge, for their financial support. We thank Prof. F. Debenham, Dr T. G. Longstaff, Mr J. M. Wordie, and Mr Charles Elton for invaluable advice concerning the organizing of the expedition and our work in the field, Dr Adolf Hoel for much useful information and a map of the Island, and Prof. J. Stanley Gardiner and the Zoological Laboratory, Cambridge, for encouragement and the loan of zoological equipment. Our particular debt to Mr Elton is obvious from the numerous references in the text to his pioneer work on the animal ecology of Svalbard. We must also thank those specialists who undertook the identification of special groups in our collections: Mr R. B. Benson (Hymenoptera Symphyta), Mr K. G. Blair (Coleoptera), Mr W. S. Bristowe (Arachnida), Dr G. H. Carpenter (Collembola), Mr J. E. Collin (Diptera, part), Dr F. W. Edwards (Diptera, part), Dr S. Finnegan (Acarina), Mr F. W. Gurney (Crustacea), Mr E. Meyrick (Lepidoptera), Mr M. E. Mosely (Trichoptera), Dr J. R. Norman (Fish); and Dr A. J. Wilmott (Plants).

THE SHORE FAUNA OF AMERDLOQ FJORD, WEST GREENLAND

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(*With Plates* 5 *and* 6 *and* 2 *Figures in the Text*)

CONTENTS

1. Introduction

There is a great lack of thorough surveys of the seashore fauna of the Arctic regions, and consequently most of the problems under discussion are purely speculative. The standard work on the West Greenland fauna is still that of Otto Fabricius (1780) in the Frederikshaab district, about Lat. 62° N., since when there have merely been a few scattered notes, such as those of Vanhöffen (1895) at Umanak, Lat. 70° N., and of Kramp (1932) on the Hydroids collected by the "Godthaab" Expedition. On the Oxford University Greenland Expedition of 1936 I had the opportunity of attempting an intensive survey of the shore of Amerdloq Fjord in the Holsteinsborg district, Lat. 67° N., at the time of year when life is most abundant and active. Such a survey is preliminary work in a little investigated field, and is of more value than scattered collections from a wide area. It is intended to raise problems rather than to solve them.

Most of the collections have been deposited with the British Museum (Natural History), and I am indebted to the following for the identifications: Dr I. Gordon (Crustacea), Capt. A. K. Totton (Coelenterata), Dr H. A. Baylis (Turbellaria and Nemertea), Dr C. C. A. Munro (Polychaeta), Dr J. R. Norman, (Fish), Dr Milwyn-John (Echinodermata); and Mr G. Tandy (Algae).

I wish also to express my gratitude to the Committee of the Oxford University Exploration Club for making it possible for a biological party to join the expedition; to the officials of the Grönlands Styrelse and especially to Bestyrer Rasmussen of Holsteinsborg, who did so much to help us in Greenland; and to Mr Charles Elton for his advice and suggestions.

2. Methods

Collections were mostly made by hand at low tide. At the mouths of streams and in pools the water net was used, a coarse one for stirring through the sand and mud and a smaller silk plankton net in clear water to collect microscopic species. In addition a number of collections were taken by a large plankton net towed from a rowing boat or between suitable points on the shore on the flood tide.

The specimens were fixed mostly in formol spirit (45 % spirit, 5 % formalin) or in Bouin's fixative. Specimens fixed by both methods were taken of most of the Annelids, Nemertines and Turbellaria. The Nudibranchs and Actiniaria were anaesthetized in menthol. The preservative was dilute formol spirit (36 % spirit, 4 % formalin), except for some of the Molluscs, which were preserved in 4 % formalin. At the suggestion of Dr J. R. Baker glycerine was added to about 20 % concentration to the soft-bodied worms, which kept them soft for sectioning.

On sand and mud shores the spade and sieve method was used for collecting such forms as *Arenicola marina* and *Pygospio elegans*, but no quantitative work was done by this method. Quantitative estimations were made by a series of counts inside a 15 cm. square. Twenty counts were taken on each of four well defined types of shore community.

A series of water samples was taken at the various collecting grounds at different levels of the tide and at different times, and the salinities later determined. Regular temperature readings at the surface were taken throughout the collecting period.

3. General description

Amerdloq Fjord is situated near Lat. 67° N. just south of the colony of Holsteinsborg. It is some 30 miles long. It is not a fjord in the usual sense, being open to the sea at both ends. At the west it opens into Davis Strait, and eastward by a narrow channel into Ikertok Fjord to the south. The island where the outpost colony of Sarfanguak is forms the southern shore, the northern being the mainland. The shore of the latter is almost uniformly rocky. Steep slabs of dark gneiss granite, with a north-east to south-west thrust, or broken scree and talus are typical. Sand patches are few and widely separated, being found only in the small bays mostly at the mouths of streams. They are rarely as much as 200 m. in length. The southern shore, though not so steep, is similar.

The rise and fall of the tides varies from about 2·5 m. (8 ft.) at the neaps to 3·7 m. (12 ft.) at springs. There are two tides each 24 hr., but the times are very variable, doubtless owing to the presence of a two-way tide through the double entrance of the fjord.

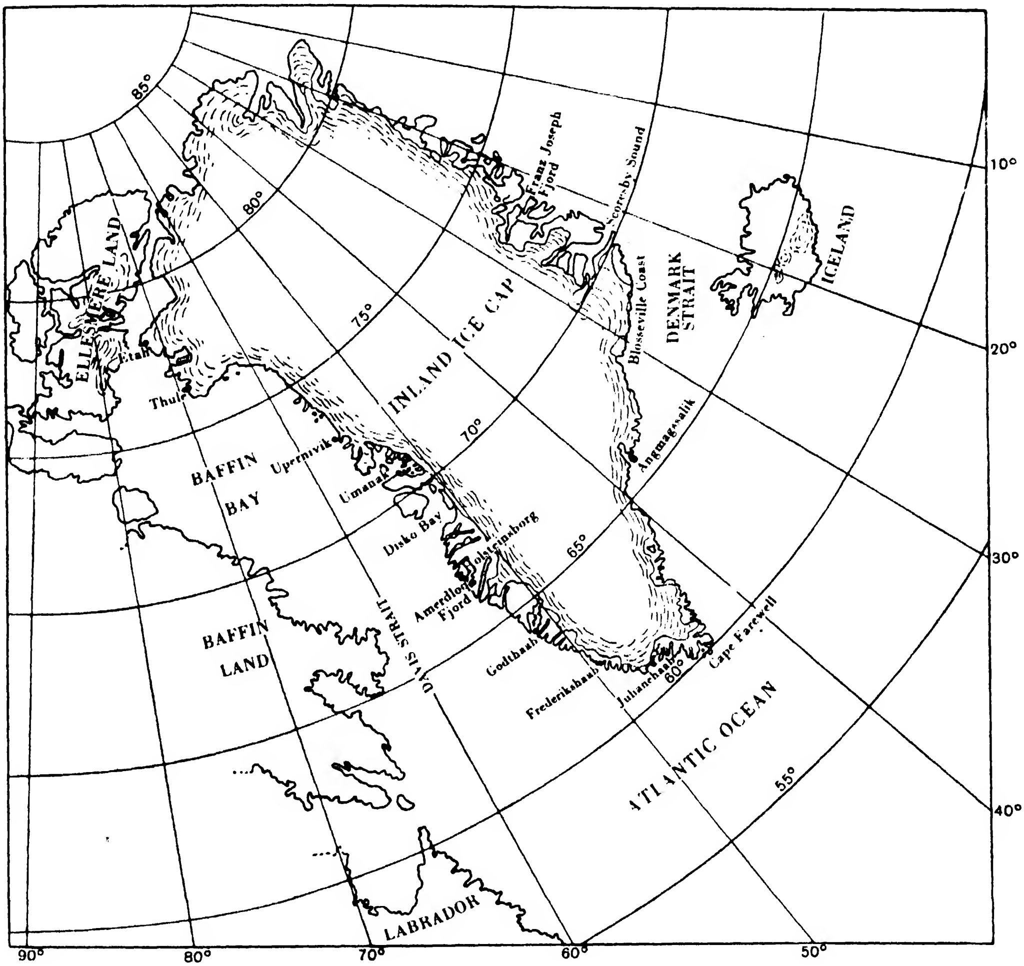


Fig. 1

The conditions therefore are comparable in certain respects with those in a sea loch on the west coast of Scotland or Ireland. A deep entrance and the absence of any large river or glacier opening into it ensure full marine conditions, while its high shores and narrow entrance provide shelter from heavy seas. On the other hand, it is normally ice covered from the end of November till April, and the ice foot, which lies along the shore may persist till well on in May. The effect of the ice on the littoral fauna is extremely important.

The collecting ground was a small bay on the north shore about 15 miles from the entrance. Here there are three stream mouths and several short

stretches of sand beach forming a break in the rocky shore. There are thus examples of each type of shore with the exception of salt marsh and lagoon, which seem to be absent from this part of the Greenland coast.

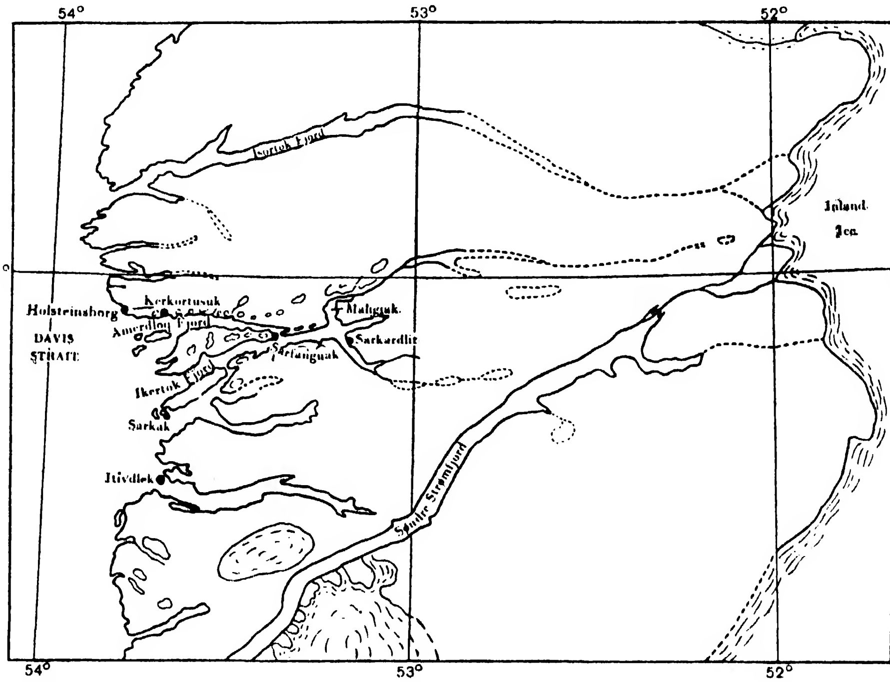


Fig. 2

4. Survey

(*a*) *Rock shore*

The bare rock shore is very poor in species, though it does support a distinct community. In the lower horizons there is often a thick growth of stunted *Ascophyllum nodosum*[1], *Fucus inflatus* and *F. vesiculosus*, on which are found large numbers of *Littorina saxatilis* var. *groenlandica*. The only other abundant species is *Balanus balanoides*, which occurs on bare as well as on weed-covered rock, and extends farther up the shore than any other species. Most of the specimens are small, and at that time of year there is a good deal of young brood. It seems likely therefore that most if not all of the individuals found on exposed rock have settled in position after the melting of the winter ice foot. Recolonization of this habitat then takes place each summer from those individuals in sheltered crevices lower down the shore or below low-water mark. That growth is very rapid during the short summer months is obvious from the enormous quantity of shed limb casings which floated on the edge of the flood tide.

[1] Species authorities are given in the table on p. 61.

Phot. 1. Rock facies: sheltered spot with thick growth of *Ascophyllum nodosum*. Colonized mainly by *Littorina saxatilis* and *Balanus balanoides*.

Phot. 2. Sand beach: upper beach, showing lines of drift weed.

Associated with this *Balanus balanoides*—*Littorina saxatilis* community are found a few other species in relatively small numbers. *Mytilus edulis* occurs in sheltered crevices and attached to the base of weed masses. *Gammarus locusta* and *Jaera albifrons* are also found, mostly under loose stones and in crevices. In the bottom of cracks and crevices small Oligochaeta spp. (*Enchytraeus* and *Lumbricillus* spp.? unidentified) and occasional specimens of the Turbellarians, *Procerodes lobata* and *Procerodes ulvae* and of the Nemertine, *Lineus ruber* are found.

In particularly favoured spots and near extreme low-water mark the following species sometimes occur: the Nudibranchs, *Onchidoris fusca* and *Acmaea testudinalis*, the Hydroid, *Laomedea flexuosa* and the Actinian, *Bunodactis stella*, and the Polychaeta, *Eteone longa*, *Phyllodoce groenlandica* and *Eulalia viridis*. The last two are represented by only one or two specimens each, and seem to be visitors from deeper water. All these species are associated with the *Mytilus edulis* bed community, but are the only ones which extend to the rock also.

The series of 20 counts inside a 15 cm. square gave the following results:

	Mytilus edulis	*Littorina saxatilis*	*Balanus balanoides*	Other spp.
1	3	21	75 + brood	—
2	2	46 (small)	117	—
3	1	29	81 + brood	*Gammarus* 3, *Jaera* p.
4	0	31	47 + brood	—
5	1	35	91	*Gammarus* 1
6	1	20	87 + brood	—
7	0	26	102	—
8	0	19	65	—
9	5 (crevice)	19	53	*Gammarus* 1, *Jaera* p.
10	0	35	48	*Gammarus* 4, *Jaera* p.
11	1	25	48 + brood	—
12	0	20	69	—
13	0	18	112	—
14	0	24	81	—
15	1	20	107	—
16	0	12	71	—
17	0	26	63	*Jaera* present
18	2	31	78	*Gammarus* 5, *Jaera* p.
19	5	21	55	*Jaera* present
20	1	21	68	—
Mean	1·15	24·95	75·9	

(*b*) *Sand beach* (*pebble and shingle*)

The noticeable feature of the small sand beaches is the absence of a distinctive fauna. Burrowing worms and Molluscs are absent, and only a very few species typical of other habitats are found. On the beaches investigated there is a regular gradation of the size of sand particles from high- to low-water mark. Fine sand occurs only on the upper part (about 0·75 m. from H.W.S. downward) and is devoid of marine life. Here occur banks of washed-up seaweed sheltering the drift-line fauna. Near low-water springs the shore really consists of pebbles, and here a scanty fauna is found. Scattered *Mytilus*

edulis are attached to the larger pebbles, on which small specimens of *Balanus balanoides* may also occur. *Littorina saxatilis* var. *groenlandica* is fairly common in scattered groups. *Gammarus locusta* is found under the larger stones, and buried in the sand the Nemertine, *Amphiporus lactifloreus* and small Oligochaetes (Lumbricillids and Enchytraeids? unidentified). No other species were found, and all these occur on other types of shore also.

A series of 20 counts inside a 15 cm. square near low-water springs on a sand-pebble beach (Home Beach) gave the following results:

	Mytilus edulis	*Littorina saxatilis*	*Gammarus locusta*
1	6	1	0
2	4	4	0
3	3	0	0
4	4	8	0
5	3	2	6
6	3	0	0
7	9	0	0
8	9	1	0
9	4	0	0
10	5	1	5
11	7	8	0
12	6	3	0
13	2	1	0
14	3	2	1
15	4	2	1
16	8	0	0
17	5	2	1
18	5	1	4
19	3	0	3
20	6	3	0
Mean	4·95	1·95	1·05

(*c*) *Stream mouth*

Of three stream mouths, all essentially the same, one was investigated thoroughly. There were extensive sand and mud flats over which the fresh water ran in variable shallow wide channels at low tide. In patches there were coarse shingle and scattered large stones, on which grew the Algae, *Enteromorpha micrococca* f. *bulbosa* and *Capsosiphon aureolus,* also occasional plants of the various Phaeophyceae found along the shore: *Fucus vesiculosus, F. inflatus, Elachista fucicola, Dictyosiphon foeniculaceous,* and *Pilayella littoralis.*

The sloping sides of the stream mouth formed a distinct zone. Here there were moraine boulders and large stones with a thick growth of *Fucus* spp. and *Ascophyllum nodosum.* Here were beds of *Mytilus edulis* near low-water springs.

The salinity of the surface water was naturally lower round the stream mouth than elsewhere. It varied from almost zero (0·08) at low tide to 3·60 g./mille at high water. It may be important however that during the winter months these streams cease to flow, and then the salinity at such places will be the same as that of the open fjord. The temperature of the fresh water was not observed to differ greatly from that of the fjord water. The latter was more variable (see daily readings), whereas the former was relatively constant between 6·5 and 8·5° C. The stream water had a *p*H of 6·6.

The fauna of both zones was essentially similar, though the relative numbers of the species was variable. On the stones and in the beds of *Mytilus edulis* along the sloping sides both *Littorina saxatilis* var. *groenlandica* and *Balanus balanoides* were present in fairly large numbers, the latter mostly as young brood. Single scattered specimens of *Balanus* occurred on stones far up the

Surface water and air temperature readings at Amerdloq Fjord, June and July 1936

N.B. Readings taken daily at 21.00 hrs.

Date	Water °C.	Air °C.	Date	Water °C.	Air °C.
25 June	5·2	4·4	11 July	12·9	9·4
26	8·5	18·9	12	12·9	11·9
27	7·7	7·4	13	12·7	10·2
28	7·7	5·5	14	12·1	7·1
29	10·2	9·1	15	11·6	7·1
30	8·8	6·0	16	13·5	10·7
1 July	11·9	13·5	17	14·8	12·7
2	10·7	7·4	18	9·9	7·4
3	11·0	8·8	19	11·0	10·2
4	12·2	17·0	20	13·8	12·4
5	12·2	9·6	21	11·9	6·6
6	8·5	5·5	22	9·4	6·6
7	9·4	7·1	23	9·4	7·7
8	6·9	6·9	24	10·1	12·1
9	9·9	7·7	25	12·4	14·8
10	10·2	8·8			

mouth of the stream, in water that must be always practically fresh. A series of 20 counts of these three species taken in this habitat gave the following results:

	Mytilus edulis	*Littorina saxatilis*	*Balanus balanoides*		*Mytilus edulis*	*Littorina saxatilis*	*Balanus balanoides*
1	14	12	1	11	9	5	Brood
2	12	8	6	12	10	4	Brood
3	15	3	100 brood	13	12	8	1 + brood
4	15	6	8 + brood	14	13	6	18 + brood
5	21	5	12 + brood	15	10	7	Brood
6	11	15	1	16	13	8	25 + brood
7	13	11	Brood	17	7	8	Brood
8	18	3	Brood	18	7	6	Brood
9	13	5	2 + brood	19	11	7	3 + brood
10	14	11	4 + brood	20	8	9	0
				Mean	12·30	7·65	

Other species present in this zone were *Gammarus locusta* and *Pseudalibrotus littoralis*, and the Isopod, *Jaera albifrons*. Under stones and buried in the sand and mud were the Polychaetes, *Capitella capitata* and *Pygospio elegans*. The latter, however, was far more numerous in the sand flat zone, where the former was correspondingly rarer. In addition there occurred small Lumbricillids and Enchytraeids, and occasional specimens of *Lineus ruber*.

On the sand flats the most noticeable feature was the enormous number of *Pygospio elegans* turned up by digging. Other sand burrowing Polychaetes present were *Capitella capitata*, *Laonice cirrata* and *Cistenides hyperborea*—1 specimen. The last was common, however, in the sand and mud of the *Mytilus edulis* beds some 600 m. distant. In the fresh-water streams running over the sand occurred *Gammarus locusta* and *Pseudalibrotus littoralis*, and on scattered stones were occasional specimens of *Mytilus edulis*, *Littorina saxatilis* var. *groenlandica*, and *Balanus balanoides*. *Arenicola marina*, which was common in the *Mytilus* beds, was absent from the stream mouth sands.

(*d*) Mytilus edulis *beds*[1]

At one particularly sheltered spot extensive beds of *Mytilus edulis* were exposed at low tide, extending vertically about 0·75 m. up from L.W.S. The flat area of sand and mud, with scattered stones and boulders and shallow tidal pools, was thickly covered with *Mytilus*. A series of 20 counts inside the 15 cm. square showed an average of 304·2 individuals per count. Here was found the richest fauna of the shore. The species may be divided roughly into those living in the open on *Mytilus* or attached to weed or to rocks, and burrowing forms found in the sand and mud under stones. The division is by no means clear cut, and many of the former especially showed a wide range in their habitats.

The following species were associated with *Mytilus* in the open. *Balanus balanoides* occurred on every rock and stone and even on large *Mytilus*. On small boulders where *Mytilus* occurred only in a band at the level of the surrounding sand, *Balanus* was scattered over the top as well. *Acmaea testudinalis* and *Cingula aculeus* were common both on *Mytilus* and on open rock in sheltered places, as were also the Actinians, *Bunodactis stella* and *Acthelmis intestinalis*. On sheltered rock, but not usually on *Mytilus* were *Onchidoris fusca* and *Laomedea flexuosa*.

Littorina saxatilis var. *groenlandica* occurred everywhere, on *Mytilus*, rocks, weed and in pools, and *Cingula aculeus* on rocks and weed. Single specimens of an Aeolid (unidentified) and of *Buccinum undatum* (var.) and *Hyas coarctatus* were obtained, the first on *Rhodymenia palmata* in a pool, the other two in rock crevices. *Phyllodoce groenlandica* and *Eulalia viridis* occurred in rock crevices.

Associated more closely with *Mytilus*, living in the shelter of the closely packed beds were *Jaera albifrons*, *Skeneopsis planorbis*, the Polychaetes, *Eteone longa*, *Nainereis quadricuspidata* and *Harmothoe imbricata*. The last occurred under stones, and really belongs to the sand-burrowing forms. In the same habitat were found *Lineus ruber*, *Amphiporus lactifloreus*, and *Notoplana kükenthali* in close-packed *Mytilus* on the under sides of stones. *Lacuna vincta* and *Margarites helicina* occurred mostly on *Rhodymenia palmata* in the pools.

In pools among the weed and sheltering under stones occurred *Pholis gunnellus*. This is interesting, for though *P. gunnellus* is found on both sides of the Atlantic, the species usually recorded from Greenland is *P. fasciatus*. Mr J. R. Norman of the British Museum, who identified it, is inclined to regard the latter as a mere variety of the common species *P. gunnellus*.

In contrast to the rest the following species were almost purely burrowing forms, found buried in the sand and mud mostly under stones and boulders. In open patches more or less free from *Mytilus* occurred *Arenicola marina* in considerable numbers. Other *Polychaetes* were the Terebellid *Polycirrus*

[1] In this area the salinity varied between 7·54 and 27·65 g./mille according to the state of the wind, tide and the amount of fresh water brought down by the stream. In the open fjord it was 33·42 g./mille.

Phot. 3. Stream mouth: upper part, showing boulder beach.

Phot. 4. Beds of *Mytilus edulis*. Stone turned on end to show line of attachment of *Mytilus edulis*: *Balanus balanoides* on upper surface.

medusa, Cistenides hyperborea, Harmothoe imbricata and *Glycera capitata* single specimen. The Nemertea, *Lineus ruber* and *Amphiporus lactifloreus* mentioned above also occurred, and in addition *Amphiporus angulatus*. The Holothurian, *Chiridota laevis*, was fairly common under large stones.

The series of 20 counts taken on the beds of *Mytilus edulis* gave the following results:

	Mytilus edulis	*Littorina saxatilis*	*Cribrina spitzbergensis*	*Acmaea testudinalis*	*Gammarus locusta*	*Nainereis quadricuspidata*	*Lineus ruber*
1	269	8	1	0	0	0	2
2	359	1	0	0	0	1	0
3	314	11	0	1	0	0	0
4	330	29	1	0	2	0	1
5	279	11	0	0	1	1	1
6	361	14	2	1	0	0	0
7	290	7	0	0	0	5	6
8	222	8	8	1	0	0	0
9	318	6	4	0	0	0	2
10	254	13	0	0	0	0	2
11	368	8	4	0	0	2	0
12	347	23	0	0	0	0	1
13	337	11	1	3	0	4	1
14	253	6	0	0	0	0	5
15	314	16	1	0	1	0	0
16	353	10	0	0	2	2	1
17	280	19	1	0	1	0	2
18	357	15	1	0	1	0	0
19	178	17	0	1	0	6	0
20	301	17	0	0	1	1	0
Mean	304·2	13·05	1·2	0·35	0·45	1·1	1·2

(*e*) *List of the total number of species and their relative abundance in different habitats*

a. = abundant, c. = common, f. = frequent, r. = rare, – = absent.

Species	Habitat			
	Rock	Sand	Stream mouth	*Mytilus* beds
COELENTERATA				
Laomedea flexuosa Alder	f.	–	–	f.
Bunodactis stella (Verr.)	f.	–	–	c.
Acthelmis intestinalis (Fabr.)	f.	–	–	c.
NEMERTEA				
Amphiporus lactifloreus (Johnston) (*A. groenlandicus*?)	–	f.	–	c.–a.
A. angulatus (Fabr.)	–	–	–	f.
Lineus ruber (Müll.)	f.	–	f.	a.
TURBELLARIA				
? *Notoplana kükenthali* (Plehn)	–	–	–	c.
Procerodes lobata (Schmidt)	f.	–	–	– ? probably present
P. ulvae (Schmidt)	f.	–	–	– ? probably present
POLYCHAETA				
Eteone longa (Fabr.)	r.	–	c.	a.
Nainereis quadricuspidata (Fabr.)	–	–	–	c.
Capitella capitata (Fabr.)	–	–	c.	c.
Harmothoe imbricata (Linn.)	–	–	–	f.
Cistenides granulata (Linn.)	–	–	r.	f.
Pygospio elegans Claparède	–	–	a.	f. ?
? *Laonice cirrata* (Sars)	–	–	f.	–

Species	Habitat: Rock	Sand	Stream mouth	*Mytilus* beds
POLYCHAETA (*cont.*)				
Polycirrus medusa Grube	–	–	–	f.
Ophelia limacina (Rathke)	–	–	–	r.
Glycera capitata Oersted	–	–	–	f.
Arenicola marina (Linn.)	–	–	–	f.
Phyllodoce groenlandica Oersted	r.	–	–	r.
Eulalia viridis (Müller)	r.	–	–	r.
CRUSTACEA				
Gammarus locusta (Linn.)	c.	c.	?	c.
G. duebeni Lilljeborg	–	–	a.	–
Pseudalibrotus littoralis (Kröyer)	–	–	a.	–
Jaera albifrons Leach	c.	–	–	c.
Hyas coarctatus Leach	–	–	–	r.
Balanus balanoides (Linn.)	a.	f.	c.	a.
MOLLUSCA				
Littorina saxatilis var. *groenlandica* (Olivi)	a.	c.	c.	a.
Onchidoris fusca (Müller)	f.	–	–	f.
Acmaea testudinalis (Müller)	c.	–	–	c.
Buccinum undatum var. (Linn.)	–	–	–	r.
Cingula aculeus Gould	–	–	–	c.
Skeneopsis planorbis (Fabr.)	–	–	–	f.
Mytilus edulis (Linn.)	f.–c.	f.–c.	r.	a.
Aeolidae sp. (unidentified) 1 spec.	–	–	–	r.
Lacuna vincta Mont.	–	–	–	f.
Margarites helicina Fabr.	–	–	–	r.
Lamellibranch, unidentified, 1 spec.	–	–	r.	–
ECHINODERMATA				
Chiridota laevis (Fabr.)	–	–	–	f.
VERTEBRATA				
Pholis gunnellus (Linn.)	–	–	–	f.
ALGAE				
Rhodymenia palmata (Linn.)				
Porphyra miniata Ag. emend. Rosenberg				
Ascophyllum nodosum (Linn.), le Jolis				
Fucus inflatus Linn.				
F. vesiculosus Linn.				
Chordaria flagelliformis (Muell.), Ag.				
Dictyosiphon foeniculaceus (Huds.), Grev.				
Elachista fucicola (Velley), Aresch.				
Pilayella littoralis (Linn.), Kjellem				
Monostroma fuscum (Post. & Rupr.), Wittr.				
Entermorpha micrococca f. *bulbosa* Collins				
Capsosiphon aureolus (Ag.) Gobi				

N.B. All species of Algae except the last two occurred on the rock and *Mytilus* bed habitats. The *Enteromorpha* and *Capsosiphon* spp. occurred in the water of low salinity of the stream mouth. From this station however the following species were absent: *Rhodymenia palmata*, *Porphyra miniata*, *Ascophyllum nodosum*, *Chordaria flagelliformis* and *Monostroma fuscum*.

In addition to the above list small Oligochaetes occurred in variable numbers in all habitats. They were more numerous in the sand and mud under the stones in the *Mytilus edulis* beds and at the stream mouth than on the sand or rock shores, and in all cases were more numerous farther up the shore than near low-water springs. Though unidentified they almost certainly belong to the species *Enchytraeus albidus* (Henle), *Lumbricillus lineatus* (O. F. Müller), and *L. minutus*.

The total number of species found in the intertidal zone is 43, allowing for

at least two species of Oligochaeta, and the numbers occurring in the four habitats investigated as follows:

Rock: 18.
Sand-shingle: 7.
Stream mouth: 14 or 15.
Mytilus edulis beds: 37, minimum (probably 40).

5. DISCUSSION

It is obvious that any discussion of zoogeographical regions must ultimately refer to the physico-chemical conditions under which the animals live, but in an ecological survey a study of the climatic conditions affecting the community is the nearest approach possible to such an analysis. In the case of the littoral community the factors which seem to require consideration are: (1) the temperature of the water; (2) the duration of exposure between tides; (3) the salinity of the water; (4) the intensity of sunlight.

Of course there are a great number of aspects of these factors which may under certain conditions be important; for instance the difference between the air and water temperatures, if extreme, may decrease the maximum period of safe exposure, or again the amount of absorption of sunlight differs greatly on white sand and black rock. It is therefore in a sense false policy to treat these factors as separate entities.

In an Arctic community the important aspects of temperature are the length of time for which the coast is ice-bound each year. the length of the period when temperatures are high enough for active life and growth, and the maximum reached during that period. The duration of the ice covering in Amerdloq Fjord is very variable from year to year. In the more sheltered inland waters such as Maligiak Fjord there may be a solid covering as early as October, and though rather later, Amerdloq is usually frozen by December. It remains solid till the end of April, and is not finally gone till June. The ice foot, which is the solid ice along the shore not rising and falling with each tide, persists longest, and naturally is the inhibiting factor for the littoral fauna. In particularly severe springs, such as that of 1918, it has remained till the end of June. As the first night frosts occur again in September, it is reasonable to suppose that fairly severe freezing will affect the littoral at low tide towards the end of that month, even before the solid winter ice sets in. Thus there is approximately a 3–4 month period more or less completely ice free and a 5–6 month period when the ice covering is solid.

It is worth comparing these conditions with those found by Madsen (1936) between Lat. 70° and 74° N. on the east coast of Greenland. Here the ice in the fjords did not break up till July or even the beginning of August, and began to form again by the middle or end of September, thus giving an ice-free period of not more than 2 months. The greater severity of conditions is reflected in the comparative poverty of the littoral fauna in this district.

Extreme differences in temperature between the water and air may be important in relation to the safe period of exposure. Though the water temperatures cannot fall much below 0° and can hardly ever rise above 15° C., the air obviously shows a much greater range. July maximum temperatures in the sun must rise well over 40°; and though no records are available from Holsteinsborg, the monthly temperature readings from Agto in Lat. 67° 57′ N. show an average of −18·7° C. Of course the minima must be a great deal lower.

Weather Records, West Greenland, 1934

N.B. There are no records of precipitation in the Holsteinsborg district for 1934, but that at Kornok may be regarded as approximately the same as would occur in Amerdloq Fjord.

Agto, Lat. 67° 57′ N., Long. 53° 45′ W., Holsteinsborg district.

	Average temp. (° C.)		Average temp. (° C.)
January	−11·8	July	6·4
February	−18·7	August	6·2
March	−17·3	September	3·5
April	—	October	−1·8
May	−1·8	November	−4·5
June	3·7	December	−7·4

Kornok, Lat. 64° 26′ N., Long. 50° 58′ W., Godthaab district.

	Average temp. ° C.	Precipitation (mm.)		Average temp. ° C.	Precipitation (mm.)
January	−8·9	25	July	10·9	22
February	−9·2	58	August	9·0	8
March	−8·1	6	September	3·0	38
April	0·3	54	October	−0·6	55
May	1·2	6	November	−3·0	53
June	8·0	1	December	−5·9	5

Total precipitation for year 331 mm.

The most obvious difference between this Arctic fauna and that of Boreal or Temperate regions is in the vertical distribution of the animals on the shore. Thus on all the different types of shore studied there is a zone, extending roughly from low-water neaps to the line of drift weed, which is almost bare of life. The only species which occur there in any numbers are *Littorina saxatilis*, Oligochaetes and *Balanus balanoides*. As this bare zone is almost certainly due to the action of the winter ice foot, the occurrence of the last species is of some interest. *Littorina* and the Oligochaetes are capable of arriving there by independent movement after the ice has melted, though the latter may possibly survive the winter buried deep in the sand.

As regards *Balanus balanoides* however the question is whether individuals survive the winter frozen in the ice foot, or whether the whole zone is colonized afresh each summer. There appears to be no direct observation on this point, or on the resistance of *Balanus* to freezing, but certain features noticed during the collecting period (July) give reason to believe that the latter is the case. In the first place all the individuals were small, those on the more exposed places

especially so, and there was a great deal of *spat*, freshly settled. That growth during the short summer period is extremely rapid is shown by the enormous quantities of shed limbs, which floated on the edge of each flood tide. On the other hand, occasional specimens occurred in exceptionally sheltered situations, such as deep fissures in the rocks, which were a good deal larger than the average. These may well be survivors from the year before. They were more frequent near low water than higher up the shore, where there is more likelihood of free water below the winter ice. It is therefore suggested that as a whole the zone occupied by the ice foot is recolonized each spring by the brood of those individuals which survive round about low-water springs and those few occupying especially sheltered positions.

This is in direct contrast with the state of affairs obtaining in temperate waters. Runnström (1925) found that at Bergen the cypris larvae settle on the rocks in April, but the ovaries did not mature till the end of the following year, and the next generation of larvae were liberated the third spring. Most of the adults then died. Hatton & Fischer-Piette (1932) observed that at St Malo the greatest numbers of larvae settled on the most exposed places, and near low-water mark. The period of maximum growth was from April to June, and practically nil during the rest of the year. Moore (1934) confirmed these results at Port Erin, Isle of Man, noting also that larvae which settled in July had no period of rapid growth that year. He found a maximum life period of 5 or 6 years.

Comparing the sizes attained by *Balanus* at St Malo (Lat. 49° N.), Port Erin (Lat. 54° N.) and Bergen (Lat. 60° N.), he found the more northerly specimens to be the larger, those at Bergen being approximately twice as large as those at St Malo, both at the ends of their first and second years. Also at Port Erin Moore found the mortality each year to be greater in the mid-tide region than near high water: 35 and 3% respectively.

Now these conditions are certainly reversed in the Arctic. At Amerdloq *Balanus balanoides* was smaller than British specimens, and, as mentioned above, was more numerous near low water than higher up the shore. This agrees with the findings of Hatton & Fischer-Piette at St Malo. It seems likely therefore that the optimum conditions for the development of *Balanus balanoides* in the littoral are satisfied in the more northerly regions of Boreal waters, possibly even in the Subarctic. Thus both St Malo, and to a lesser extent Port Erin, are to the south of this optimum, while Amerdloq Fjord is to the north. The conditions at Bergen may be some where near the optimum, but in the absence of further observations it is impossible to delimit it more accurately.

Huntsman (1919) records the occurrence of *Balanus* between 4 and 22·5 ft. above low water on a 25 ft. vertical tide in the Bay of Fundy, and also from low water to about 4 ft. on a 4·5 ft. tide on Cape Breton Island. He gives no measurements of size, but his observations show the occurrence of the species throughout the tide range under more severe conditions than at Bergen. Cape

Breton Island at least is ice-bound during some of the winter months. His observations were made in July, and unfortunately he made none of the mortality during the winter.

Obviously if the northern distribution of *Balanus balanoides* is limited by the duration and thickness of the ice foot, it is necessary to determine the resistance of the species to freezing. This is an unsolved question, but there is every reason to believe that a protracted ice foot is fatal. Gurjanova *et al.* (1930) found *Balanus* could survive periods of severe frost up to 48 hr., but Aurivilius (1895) showed that in the Baltic the adults could not survive protracted freezing, certainly not over several weeks, though here the nauplii at that period lie free in the mantle cavity and appear to survive the death of the parent. For the present however the most rational hypothesis is that the northern limit of *Balanus balanoides* is determined by the length and duration of the ice foot.

The reasons for the decline in the species in more southern Boreal waters is more obscure. The most promising line of approach is to attempt to correlate the rate of growth with both the water temperatures and with the length of daylight in different latitudes. As most of the growth takes place in the early summer months, when days are lengthening, it is natural that it should be greatest in more northerly waters, where the length of daylight increases more rapidly during these months, and the total number of hours of sunlight is greater. What connexion this may have with the capacity to withstand exposure to desiccation in the air, for at St Malo most of the specimens occurred near low water, is obscure. The southern limit of the species in European waters is Portugal (Stephensen, 1936).

The recolonization of the ice-foot zone by *Littorina saxatilis* and *Balanus balanoides* each year is a special case of what appears to be general of the Arctic littoral. Thorson (1934) records such species as *Harmothoë imbricata*, *Phyllodoce groenlandica* and *Saxicava arctica* from depths between 3 and 14 m. in the Scoresby Sound and Franz Joseph Fjord, which lie between Lat. 70 and 73° N. on the east coast. Again Summerhayes & Elton (1923) found *Capitella capitata*, *Harmothoë imbricata*, *Ophelia limacina*, *Pseudalibrotus littoralis* and *Gammarus* sp. in depths of 1–3 m. in Lat. 78° 40′ N. on the west coast of Spitsbergen. All these species occurred in the littoral at Amerdloq though in the cases mentioned they were a good deal north of their limit in this community. None of them has been recorded from the littoral north of Angmagssalik (Lat. 66° N.) on the east coast of Greenland, and not at all from Spitsbergen.

There do not appear to be any similar observations of species extending their northern range in the sublittoral from the West Greenland coast, but during the collecting period a marked shoreward migration was noticed in the month of July. Thus certain species, which were uncommon at the spring tides at the end of June, were far more numerous at the next ones a month later.

Onchidoris fusca, Chiridota laevis, Pholis gunnellus, Amphiporus angulatus, Acmaea testudinalis and *Laomedea flexuosa* were particularly noticeable in this respect, though no counts were made. The increase in the numbers of *Balanus balanoides* has already been mentioned.

Madsen (1936) has distinguished Arctic and Subarctic (or Boreo-Arctic) areas in the northern littoral. The southern limit of the former is defined as the most northerly stations of *Balanus balanoides* and of marine Molluscs in the intertidal zone, and of the latter as the southern limit of two typically Arctic species of Crustacea, *Mysis oculata* and *Pseudalibrotus littoralis*. Thus the Boreo-Arctic area is that in which Molluscs, *Balanus, Mysis* and *Pseudalibrotus* may all occur together. The heuristic value of such a division depends on the world-wide association of these species in the same relation. Thus for the distinction to have any significance it is necessary to show that the southern limits of *Mysis oculata* and *Pseudalibrotus* more or less coincide throughout the world, and the same of the northern limits of *Balanus balanoides* and the Molluscs to which Madsen referred—*Mytilus edulis, Acmaea testudinalis, Littorina saxatilis*.

There is evidence that on the east coast of Greenland there is a sudden and marked climatic change between Lat. 66° and 70° N. The submarine ridge between Iceland and Greenland is here shallowest, and divides the cold water of the Polar sea from the warmer Atlantic water. It is only south of this ridge that the Irmiger current, a branch of the Gulf Stream, makes its influence felt (Iversen, 1936, in Degerbøl, 1937). The climatic changes associated with this are considerable, the difference between Scoresby Sound (Lat. 70° N.) and Angmagssalik (Lat. 66° N.) being described by Vahl & Hatt (1923), as that between a high or dry continental Arctic and a low maritime Arctic or North Atlantic climate. For corresponding climatic differences on the west coast, where there is no such sudden separation of Arctic and Atlantic waters, a distance over twice as far is required, from Upernivik (Lat. 73° N.) to Godthaab (Lat. 64° N.).

Madsen places the northern limit of his Subarctic area on the east coast to the north of Angmagssalik, probably on the Blosseville Coast round about Lat. 68° N. This area has also been regarded by Degerbøl (1937) as a zoogeographical dividing line for the land fauna as well. The extremely unfavourable conditions on this coast, where numerous large glaciers descend into the sea, may well form a limit to the northern distribution of *Balanus balanoides* and of littoral Molluscs. At Upernivik, which enjoys almost the same climate as Scoresby Sound, they still occur in the littoral (Vinterberg *cit.* Madsen), and their northern limit on the west coast has not yet been found. It is unlikely, however, that Molluscs extend as far as Cape York (Lat. 76° N.). *Balanus balanoides* has been recorded in the littoral from Lat. 78° N. on the west coast (Stephensen, 1936), which is a good deal farther north than littoral Molluscs may be expected.

The crucial point therefore in determining the value of Madsen's division is whether it can hold for a coast on which the climatic change is one of gradually increasing severity to the north, without any such barriers as that of the Blosseville Coast. It should be possible to settle this by a careful study of the littoral of West Greenland from Upernivik northward.

An alternative, and probably more satisfactory, method of testing the value of such zoogeographical divisions is by an examination of the world wide distribution of all the species concerned. If a large block of species can be associated as always occurring together, and their distribution correlated with a certain range of climatic conditions, then such a term as Subarctic may be of use. Of the species found at Amerdloq Fjord, the distribution of *Hyas coarctatus* may be regarded as typical. It has been recorded from the west coast of Greenland as far as 70° 30′ N., but not from the east coast; in North America from the New England coast to the north of Labrador, and from Hudson Bay; from the Mackenzie River mouth, Alaska, Bering Straits and as far south as Korea; in Siberia from Bennett Island, Lat. 77° N., Long. 150° E.; from west Iceland, south and west Spitsbergen, the Faroës, Shetlands, and the Scandinavian coast as far east as the White Sea. It is not known from Lats. 60–135° W., or from 49–150° E., but these are little known areas (Rathbun, 1925).

Such a circumpolar distribution is general for the species occurring in Amerdloq Fjord, many showing a good deal wider range. The British and New England coasts in particular seem to be the southern limit of a large number. For instance all the Molluscs found at Amerdloq also occur off New England (Johnson, 1915), and the following at least in Britain; *Acmaea testudinalis*, *Buccinum undatum*, *Cingula aculeus*, *Lacuna vincta*, *Margarita helicina*, *Littorina saxatilis* and *Mytilus edulis* (Posselt, 1898). The same circumpolar distribution is true for the Polychaetes, *Harmothoë imbricata*, *Eulalia viridis*, *Phyllodoce groenlandica*, *Eteone longa*, *Glycera capitata*, *Arenicola marina*, *Capitella capitata* and *Ophelia limacina* (Ditlevsen, 1914). As shown by Madsen, *Mysis oculata* and *Pseudalibrotus littoralis* have a rather more northern distribution, but *Jaera albifrons* is rather more Boreal (Zirwas, 1910, *cit.* Stephensen, 1913). *Bunodactis stella* is a rather more Arctic species, having been recorded from Lat. 72° N., on the east coast of Greenland, from east Spitsbergen and from Siberia, nor does it occur south of the Faroës in the European or Cape Cod in the American zone.

Laomedea flexuosa has only once been recorded from Greenland, on the south-west coast (Kramp, 1932), and has a more southerly range than most of the other species, extending from the Mediterranean to the Lofoten Islands in Europe; also from south Iceland and New England. The distribution of *Chiridota laevis* is restricted and little known. It is only known from south-west Greenland, north-east America, Spitsbergen, the Kara Sea and Bering Strait, but not from east Greenland, Iceland or Europe (Mortensen, 1913). *Pholis gunnellus* occurs on both British and American coasts.

In view of the extremely wide range of most of the species mentioned it does not appear profitable to use the term Subarctic as descriptive of the fauna as a whole. In other words it is undesirable to use the geographical limits of one or two species for establishing zoogeographical areas, unless they can be correlated with sudden climatic changes, such as the thermocline. As most of the species found at Amerdloq occur also on the British coast and in Spitsbergen, the latter having more rigorous Arctic conditions than the Holsteinsborg district of Greenland, Madsen's Subarctic zone is without significance.

6. SUMMARY

1. A description is given of the littoral fauna of Amerdloq Fjord, Lat. 67° N., West Greenland, during the month of July.

2. The district possesses a rich and varied fauna, composed mainly of species with a circumpolar distribution, and extending in many cases as far south as the British Isles in Europe and the New England coast in North America.

3. Four types of shore are treated separately, namely rock, sand, mouth of a stream, and beds of *Mytilus edulis* on mud, and a series of counts was made of the numbers of individuals of different species occurring within a 15 cm. square from each.

4. It is noticed that the upper levels of the intertidal zone is practically bare of life, and this is attributed to the action of the winter ice foot, which in this district persists for some 6 months in the year. The limiting influence of the ice foot is discussed with special reference to the distribution of *Balanus balanoides*.

5. The usefulness of delimiting a Subarctic area in the littoral, as recommended by Madsen (1936) is discussed. It is concluded that in view of the wide distribution of the majority of the species concerned, such a zoogeographical division is without value, unless it can be restated in physiological (climatic) terms.

REFERENCES

* Not verified in the original

Aurivillius, C. W. S. (1895). Öfvers. Vetensk Acad. Förh., Stockh. 52: 133–50.

Degerbøl, M. (1937). Medd. om Grønland, 104, No. 19: 1–36.

Ditlevsen, H. (1914). Medd. om Grønland, 23, No. 7: 659–741.

Fabricius, O. (1780). "Fauna Groenlandica." Hafniae et Lipsiae.

***Gurjanova, E., Sachs, I. & Uschakov, P. (1930).** Trav. Soc. Nat. St Pétersb. (Leningr.) 60 (2): 17–101. (In Russian; summary in German.)

***Hatton, H. & Fischer-Piette, E. (1932).** Bull. Inst. Océanogr. Monaco, No. 592: 1–15.

Huntsman, A. G. (1919). Proc. Roy. Soc. Canada, Ser. 3, 12 (1918), (sect. 4): 53–60.

Johnson, C. W. (1915). Occ. Pap. Boston Soc. Nat. Hist. 7, No. 13: 1–231.

Kramp, P. L. (1932). Medd. om Grønland, 79, No. 1: 1–86.

Madsen, H. (1936). Medd. om Grønland, 100, No. 8: 1–79.

Moore, H. B. (**1934**). J. Mar. Biol. Ass. 19: 851–68.
Mortensen, T. (**1913**). Medd. om Grønland, 23, No. 2: 299–379.
Posselt, H. J. (**1898**). Medd. om Grønland, 23, No. 1: 1–298.
Rathbun, M. J. (**1925**). Bull. U.S. Nat. Mus. 129.
Runnström, S. (**1925**). Bergens Mus. Aar. 5: 1–46.
Stephensen, K. (**1913**). Medd. om Grønland, 22, No. 1: 1–479.
Stephensen, K. (**1936**). Medd. om Grønland, 80, No. 2: 1–38.
Summerhayes, V. S. & Elton, C. S. (**1923**). J. Ecol. 11: 214–86.
Thorson, G. (**1934**). Medd. om Grønland, 100, No. 3: 1–68.
Vahl, M. & Hatt, G. (**1923**). "Jorden og Menneskelivet." København.
***Vanhöffen, E.** (**1895**). Bibliotheca Zoologica, 8, Heft 20: 15–22.

A CENSUS OF THE ECTOPARASITES OF SOME CEYLON RATS

By GORDON B. THOMPSON

Owing to their intimate connexion with plague a vast number of analyses of the fleas found on rats in various parts of the world have been published. As far as I am aware, however, no one has ever published a complete census of the ectoparasites occurring on a rat population. In this short paper I am presenting a complete analysis of the ectoparasites found on fifteen specimens of the common Ceylon rat (*Rattus r. kandiyanus* (Kelaart)). This rat is found everywhere in the vicinity of human habitations throughout Ceylon and it has been the subject of many investigations in connexion with the parasitology of plague (see papers by Hirst, 1926, 1927, 1933).

The whole of the material on which this paper is based was collected by Capt. W. W. A. Phillips, to whom I should like to express my thanks. Most, if not all, of the rats were trapped near his bungalow, on the outskirts of the jungle. The rats were in every case examined as soon as possible after being trapped in order to obtain the maximum number of parasites. It is possible that some of the very small mites (e.g. *Myobia* spp.) were overlooked, but otherwise it seems that the collecting was complete. The determination of the rats was done by the collector, who is a well-known authority on the mammals of Ceylon.

The ectoparasitic Arthropoda found on rats are as follows: Siphunculata (sucking-lice), Siphonaptera (fleas), Acarina (mites and ticks). Representatives of all these groups were collected from the Ceylon rats. Lice were only taken on two of the rats and this scarcity of lice is in accordance with my experience. It is interesting to note that two species are represented. *Polyplax spinulosa* (Burmeister) is the louse normally found on domestic rats wherever they occur. *Hoplopleura oenomydis* Ferris, of which only a single specimen was taken, has a very interesting distribution. It was originally described from various species of Murids occurring in British East Africa and the Philippine Islands. It has since been recorded off *Rattus* spp. from the Marquesan Islands, Federated Malay States, Queensland and Sumatra (Ferris, 1932).

With regard to the fleas, as many as twelve different species have been collected from Ceylon rats. The fact that only four of these occurred on the rats dealt with in this paper is in all probability something to do with the high altitude at which the rats were collected. Flea distribution seems to be largely controlled by environment rather than by their hosts' distribution. This is especially the case with the species *Leptopsylla segnis* Schönhr. which in Europe is extremely common on the house mouse and on rats, but in India and Ceylon

Ectoparasites of the Common Ceylon Rat (Rattus r. kandiyanus (*Kelaart*)) *from C. P. Gammaduwa, Mousakande*

		Ectoparasites								
			Siphonaptera			Acarina (mites)			Ixodoidea	
Height and date	No. and sex of rats examined	Siphunculata	*Xenopsylla cheopis* Roths.	*Leptopsylla segnis* Schönh.	*Stivalius phoberus* Jord. & Roths.	*Laelaps nuttalli* Hirst	*Laelaps echidninus* Berlese	Undetermined genera and species of mites	*Ixodes petauristae* Warburton	Total no. of parasites
Alt. 3350 ft., 6. xii. 1934	1	—	—	—	1♀	3	4	—	—	8
12. xii. 1934	1	—	—	—	1♀ 1♂	—	—	—	—	2
16. i. 1935	1	—	—	—	2♀♀ 1♂	—	10	—	—	13
22. i. 1935	1♂	—	—	—	2♀♀	—	—	—	—	2
23. i. 1935	1♂	—	—	2♀♀	1♀	—	—	—	—	3
25. i. 1935	1♂	—	—	—	1♀ 1♂	2	6	—	—	10
28. i. 1935	1♀	1♀*	1♀ 1♂	1♀	6♀♀ 3♂♂	—	—	—	—	13
29. i. 1935	1♀	—	2♂♂	—	1♀	—	—	—	—	3
Alt. 3300 ft., 13. iv. 1935	1	—	—	—	2♂♂†	—	4	—	—	6
Alt. 3400 ft., 28. vi. 1935	1♂	—	—	—	—	—	—	—	1 larva‡	1
28. vi. 1935	1	—	—	—	1♀	—	5	2	3 larvae‡	11
Alt. 3300 ft., 4. vii. 1935	1	—	—	—	1♀	3	4	—	1 nymph‡	9
5. vii. 1935	1	—	—	—	1♀	—	—	—	—	1
13. viii. 1935	1	3♀♀§	—	—	—	—	1	—	—	4
13. viii. 1935	1	—	—	—	1♂	—	—	1	—	2

* *Hoplopleura oenomydis* Ferris.

† Also one female of *Ctenocephalides felis felis* (Bouché).

‡ The nymph of *Ixodes petauristae* Warburton is at present undescribed. The larvae are doubtfully assigned to this species. Dr M. Sharif is publishing an account of the immature stages and I have to thank him for the identifications.

§ *Polyplax spinulosa* (Burmeister).

only occurs in numbers at high altitudes. Hirst (1933, p. 62) points out that *L. segnis* actually predominates on rats at Nuwara Eliga, which is situated in the Central province of Ceylon at an elevation of 7000 ft. From the results tabulated here it seems that *Stivalius phoberus* Jord. and Roths., which is a comparatively large flea and confined to Ceylon, is the commonest species on these rats. It is actually one of the indigenous rat fleas at the highest altitudes and has not been found below 2000 ft. The females are twice as common as the males. Another species of flea, *Ceratophyllus tamilanus* Jord. and Roths., peculiar to Ceylon and found commonly by Hirst (1933) on rats at high altitudes, was not taken by Capt. Phillips.

Ctenocephalides felis felis (Bouché), the common cat flea, of which only a single specimen was taken, is not very common in Ceylon and is almost totally replaced by the subspecies *orientis* Jordan which occurs commonly throughout

the Indo-Malayan regions. *Xenopsylla cheopis* (Roths.) is undoubtedly the most important flea from the point of view of plague and although it only occurred on two rats it is approximately in accordance with the percentage infestation found by Hirst (1926, 1933).

The immature stages of the tick *Ixodes petauristae* Warburton (1933) occurred on three rats and are of great interest, since up to the present only the female of this tick is known. Warburton's specimen was taken from *Petaurista philippensis lanka* (Wroughton) (Ceylon grey flying-squirrel), collected at Mousakande, Gammaduwa, C. P., Ceylon, 3350 ft., v. 1930.[1] The rat must therefore be regarded as a host of the immature stages of this tick and may thus aid in the propagation of the species.

The mites (Laelaptidae, etc.) frequently occur in very great numbers on rats. No great numbers were found on these rats. *Laelaps echidninus* Berlese is a world wide parasite of rats, whereas *L. nuttalli* Hirst seems only to be widely distributed in the tropics.

REFERENCES

Ferris, G. F. (1932). "Ectoparasites of Marquesan rats." Bull. Bishop Mus., Honolulu, **98**: 117–27.

Hirst, L. F. (1926). "Researches on the parasitology of plague, Part I." Ceylon J. Sci. (D), **1**: 155–271.

Hirst, L. F. (1927). "Researches on the parasitology of plague, Part II." Ceylon J. Sci. (D), **1**: 277–458.

Hirst, L. F. (1933). "A rat-flea survey of Ceylon..." Ceylon J. Sci. (D), **3**: 49–113.

Warburton, C. (1933). "On five new species of ticks (Arachnida Ixodoidea)..." Parasitology, **24**: 558–68.

[1] These are the correct data for the type specimen—not stated by Warburton (1933).

A SURVEY OF THE DISTRIBUTION OF THE WOOD ANT (*FORMICA RUFA*) IN ENGLAND, WALES AND SCOTLAND

By ENID NELMES

CONTENTS

1. Introduction

This enquiry was begun in 1933 in co-operation with the Bureau of Animal Population game survey, its primary aim being the construction of a map showing the distribution of wood ants in the British Isles, correlated if possible with soil and other factors. This required a consideration of glacial deposits, and as there is no complete drift map of England and Wales it was decided to include rough outlines of drift-covered areas on the distribution map, which would thus serve two purposes. The information supplied is neither detailed nor accurate enough for the map to be used for anything but a preliminary reference, but it is hoped that as such it may be of value.

Records for *Formica rufa* L. (including the varieties *alpina* and *rufo-pratensis*) were collected from various sources. A considerable amount of information was found in the publications of local Natural History Societies; some was obtained through Museums, and a great deal through the kindness of observers all over the country in sending specimens and information in answer to a question in the Bureau of Animal Population's Annual Enquiry for 1933 done by Mr A. D. Middleton. Mr Charles Elton put at my disposal notes

obtained through his Woodland Bird Survey (1930) and inserted a Note in this *Journal* (this appeared also in the *Journal of Ecology*, through courtesy of Prof. A. G. Tansley), and has also passed on records which have come to his notice from time to time. Dr O. W. Richards has identified many of the specimens and given helpful advice; Mr D. F. W. Baden-Powell has given valuable assistance with geological problems. To all of these my thanks are due, and I owe an especial debt of gratitude to Mr Elton, who suggested the survey, for continual encouragement and assistance.

A list of the localities from which records have been obtained, with a brief summary of the information available for each, is given in Table 4. The full data are being deposited in the Bureau of Animal Population.

2. CONSTRUCTION OF MAP

The coastal outline was traced from the Ordnance 10 mile to the inch Physical Map of England and Wales (1925) and the localities from which wood ants had been recorded were plotted as accurately as possible on the tracing, after their position and the nature of the underlying rock had been determined from the drift edition of the 1 in. Ordnance Geological Maps. For the Lake District, most of Wales and the South Midlands, and part of the West Riding of Yorkshire only the solid edition was available. The rock contours were transferred to the tracing by placing it over the Physical Map and copying them from the Ordnance Ten Mile Geological Map; they could not be directly traced owing to a slight discrepancy between the projections of the two maps.

Only boulder clay, and glacial sand and gravel treated together, of the glacial deposits, have been included, and their outlines have been obtained from several sources. The ¼ in. Drift Maps were used for East Anglia, and the 1 in. edition for the rest of the country except for those parts mentioned above. In order to complete the outlines in those districts an indication of drift-covered areas was obtained from the map illustrating F. W. Harmer's (**8**) paper on the distribution of glacial drift; but as this shows neither definite boundaries nor the nature of the drift, broken lines have been used for material from this source to distinguish it from the more accurately defined information obtained from the Ordnance Maps.

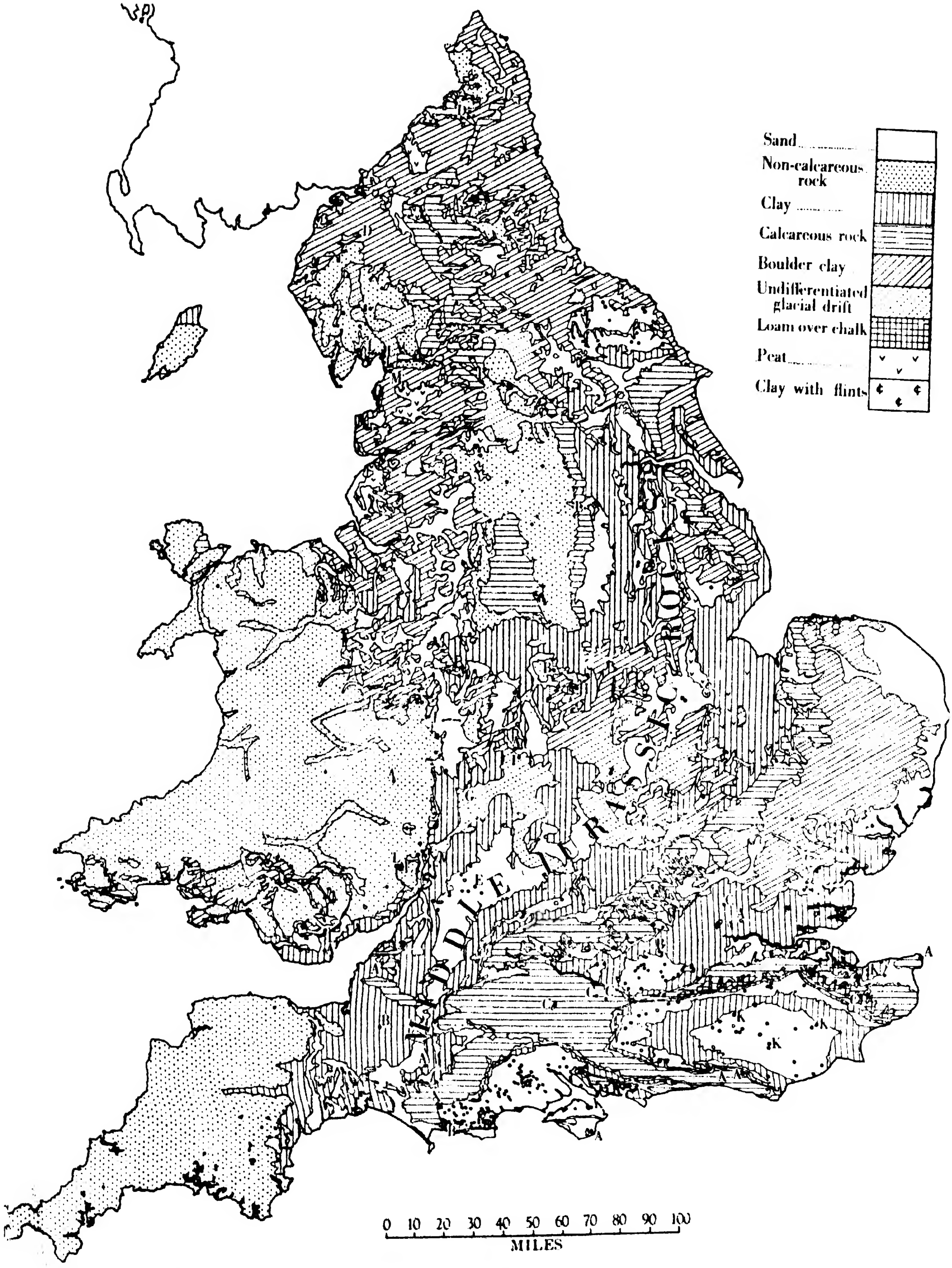
In some instances the rocks were subdivided according to the nature of the soil to which they more generally give rise and hatched accordingly, with the exception of several which vary a great deal locally. The following table shows the classification adopted, the symbols being those employed in the Ordnance Geological Maps. For the sake of brevity they have been used throughout the tables.

The Purbeck and Portland Beds and the Cornbrash have been included with the adjacent formations on the map because each occupies so small an area that on a map of this size it would be indistinguishable from the neighbouring rocks. The Upper Lias and Middle Jurassic deposits consist mostly of lime-

Table 1

Explanation of symbols

Sand		Clay		Non-calcareous rock		Calcareous rock		Unclassified	
Oligocene Beds	i^{8-11}	London Clay	i^3	Coal Measures	d^5	Chalk	h^5	Purbeck Beds	g^{14}
Bagshot Beds	i^{4-7}	Gault Clay	h^3	Millstone Grit	d^4	Carboniferous Limestone	d^{1-3}	Portland Beds	g^{13}
Oldhaven etc. beds	i^{1-2}	Wealden Clay	h^1	Culm Measures	d	Magnesian Limestone	e^{2-4}	Cornbrash	g^9
Upper Greensand	h^4	Kimeridge Clay	g^{12}	Devonian and Old Red Sandstone	c			Great Oolite, etc.	g^{6-8}
Lower Greensand	h^2	Oxford Clay	g^{10}	Upper and Lower Silurian	$-b$			Inferior Oolite	g^5
Hastings Beds	h	Middle Lias	g^2	Cambrian	$-a$			Upper Lias	g^{3-4}
Corallian Beds	g^{11}	Lower Lias	g^1	Pre-Cambrian	$-x$				
Keuper Sandstone	f^5	Rhaetic Beds	fg.	Igneous Rocks: Andesite = A., Basalt = B, Felsite = F, Granite = G, Syenite = S					
Bunter Sandstone	f^{1-3}	Keuper Marls	f^6						
Permian Marls and Sandstones	e								



A, definitel ocality not given; B, on several formations; C, possibly on glacial drift; D, sandstone; E, Cirencester Park; F, Ley Park; G, Trench Wood; H, Sheat Hedges Wood; I, Hay Wood; J, Albyn's Covert; K, records on light clay; L, possibly leached; M, Carnforth.

stone in the south and sandstone in the north, and because of this variation they have not been classified, but are indicated by the words "Middle Jurassic". All the Carboniferous Limestone has been marked as calcareous rock, but in the north of England it is composed mostly of sandstones and shales with thin bands of limestone, and so is not strictly calcareous. The Old Red Sandstone of Herefordshire and South Wales has been shown as non-calcareous rock, and no distinction has been made between the rich soil of the Plain of Hereford and the infertile soil of the Black Mountains, as a satisfactory boundary cannot be fixed between them.

Alluvial deposits have been marked as clay. Peat has been indicated where possible, sometimes within definite boundary lines, sometimes by means of scattered symbols, but no distinction has been made between that of moorland and that of fenland origin. The loam on the North Downs and the clay-with-flints on the Marlborough Downs and the Chilterns have been included where possible. River deposits have been omitted, except in some cases where they consist of large tracts of alluvium. No distinction has been made between glacial sand and that derived from underlying rocks.

It has only been possible to map England and Wales in such detail, but an outline map of Scotland on the same scale showing the distribution of wood ants has been made. The information received from Ireland is so scanty that a consideration of its wood ant population has been postponed.

Although efforts have been made to obtain a complete set of records, it is almost inevitable that some have been overlooked. Enough have been found however to give an idea of the way in which the species is distributed over the country, and additions to the list would be welcome. Localities from which reliable records have been received are indicated by solid spots, those needing confirmation by rings, and those where the ants are extinct by dots surrounded by rings.

3. Distribution of wood ants

A. *England*

From a general examination of the map the following points are apparent:

1. The records are scattered throughout the country, but are congregated in groups in certain districts and are absent from large tracts in others.

2. Most of the records are on sand or non-calcareous rock. Clay and calcareous rocks appear to be avoided.

3. On comparison with the physical map it is found that the groups of records generally correspond with hills and the slopes of river valleys, and the bare patches with low-lying ground or with moorland or mountainous regions where trees are scarce or from which they are absent altogether.

For discussion, the map of England has been divided into nine regions each containing one or more groups of records, and five with isolated or few records.

Photo F. Picknell

Phot. 1. Nest of *Formica rufa* in pine wood near Coldwaltham, Sussex.

NELMES—Wood Ant

1. *South-east region.* This includes Kent, Sussex, and the London Basin, with Essex and south-east Suffolk. Between the North and South Downs there is a series of alternating sandy ridges with numerous records, and clay lowlands with none. On the North Downs, several colonies are scattered along the loam that covers the chalk in the Rochester district. The land extending eastward between the North Downs and the Chilterns is mostly composed of London clay, and there are several isolated colonies scattered where the soil is light or gravelly, or where there is a local patch of sand, but in the west there are two large patches of Bagshot sand and on these records are concentrated in great numbers.

2. *The Hampshire basin.* This is mostly sand, but there is a narrow belt of London clay devoid of records before the northern chalk boundary is reached. On the sand wood ants are exceptionally plentiful, and the records fall into four distinct groups corresponding with the Great Heath of Dorset, the New Forest, and the districts round Wimborne and Southampton—all below 400 ft. with the exception of much of the New Forest and small patches elsewhere. This comparatively low altitude, with the large numbers of records, are features of interest found also in the Bagshot sands of the South-east region.

3. *The south-west peninsula.* This lies west of a line between Minehead and Exeter and consists of non-calcareous rocks producing moorland and hilly country. Wood ants are scarce throughout the whole peninsula but are to be found near Truro and Minehead, and on the thin siliceous soil of the valleys draining Dartmoor they are plentiful. They are said to occur commonly in the well-wooded valleys between Launceston and Falmouth, and their absence from the northern side of the peninsula is probably due to the lack of trees caused by exposure to wind.

4. *The Jurassic hills.* This includes the Cotswold range ("Middle Jurassic") with the ridge of Corallian to the south-east running parallel to it but separated from it by clay. Most of this land is under pasture and wood ants are not common. They occur sporadically along the Corallian where it is sandy or gravelly, but on the Cotswolds they are confined to one large group on the steep thickly wooded slopes of the Stroud district with one or two isolated localities in Northamptonshire. Near Stroud, despite the number of records, the ants are local and the nests few in number. They are said to occur only in woods facing south, and this may well be so since the sun is effectively cut off from valleys with a northerly aspect by the precipitous slopes facing them. The nests are invariably found in beech or larch plantations, sometimes replaced by birch scrub, on slopes on thin clay overlying oolite. Wood ants are said to be common in Cirencester Park (E), but only two nests have actually been reported from there.

In Northamptonshire the oolitic limestone is replaced by sands, and on these wood ants occur near Stamford and Northampton.

5. *The Welsh border hills.* These extend from the Bristol Channel to

Shrewsbury, and most are composed of non-calcareous rock. The Forest of Dean and the South Shropshire uplands are on poor, infertile soil derived from the Coal Measures. A belt of limestone surrounds the Forest of Dean and there are further deposits in the Malvern Hills. Wood ants occur locally in great numbers in the Forest of Dean, and at Lyth Hill near Shrewsbury where the soil is sandy, derived from glacial drift. Throughout the rest of this region they are scarce, and records generally refer to single nests.

6. *The Pennine Plateau.* This is the central plateau between Derby and the Tyne Gap. The south-eastern portion is non-calcareous rock (Millstone Grit and Coal Measures); the north-western portion is limestone for the most part covered by drift deposits. There is a strip of limestone to the east of the plateau, and a further patch in the south-west.

Wood ants are found on the slopes of the river valleys round the southern and eastern edges of the plateau on the non-calcareous rock. On the whole they are not common, being very local in distribution though often abundant were they do occur. In the West Riding in particular they are scarce, and have in recent years died out in many places where they were to be found formerly.

7. *The Lake District and North Lancashire.* This district consists almost exclusively of non-calcareous Silurian rocks with some glaciation, but there is limestone in the south. The small patch to the north marked as calcareous rock on the map is actually sandstone.

Wood ants are extremely local, as might be expected in mountainous, sparsely wooded country. They do occur in a few places, however, and in some are excessively abundant—notably Ashness Wood near Keswick, Eggerslock Wood on the southern patch of limestone, and Parkhead Wood (D). Here again the colonies are situated on hill slopes.

8. *The moorlands of north-east Yorkshire.* These form a barren plateau drained north and south by deep wooded valleys, and largely composed of sandstones of varying origin which to the north are covered by boulder clay. Oxford clay in this neighbourhood is represented by sandstones and sandy shales. Towards the heads of the valleys the underlying soft Middle and Upper Lias shales are exposed.

Wood ants are local, but have been reported from the slopes of nearly all the valleys running up into the plateau. Along the southern edge every dale has its colony, or has had in the past, but the northern valleys are apparently less suitable. The ants are especially numerous in the pine woods near Helmsley at the south-west corner of the plateau, and in the Hackness Valley near Scarborough. In other places there are a few nests, or the ants have now disappeared. As a general rule they are confined to the wooded parts, but in Baysdale and Jugger Howe Dale and on Silpho Moor the nests are among heather on open moorland.

9. *The Tyne Valley and the Cheviots.* Most of this area has been glaciated. Where the underlying non-calcareous rocks come to the surface they produce

poor infertile soils. As mentioned previously, the limestone is largely replaced by sandstone.

The only large group of records is in the Tyne valley itself, where not only is the species of frequent occurrence in pine woods on sand, but the individuals are numerous also. There are three records from the Coquet Valley where it leaves the Cheviots, several from isolated localities, but in all of these the ants appear to be uncommon with the exception of Chapel Wood, Morpeth, where they are abundant, but restricted to an area of half a square mile.

Before passing to the unfrequented areas the main points arising from the foregoing discussion may be summarized. Infertile soils—i.e. sand, or thin soil derived from non-calcareous rocks—provide the most suitable habitat. On non-calcareous rocks, wooded valley slopes are preferred before low-lying ground, but on sandy soil this is not always the case, as in Hampshire and Surrey. Generally speaking, however, wood ants are likely to be found in hilly country, provided that it is not too high to support woodland. There are very few records from limestone.

The areas from which wood ants are conspicuously absent may now be considered.

1. *The Midland Plain.* This occupies an intermediate position, for records do occur within the area, though not in the plain itself. It forms a rough triangle between the southern edge of the Pennines and the Cotswold escarpment, extending south-west to the Bristol Channel, westward to the Welsh border hills, and north-east to join the Great Clay Vale at Lincoln. This limit is more apparent on a physical map, for at Lincoln the Jurassic rocks fall away to 200 ft. and under, but it coincides approximately with the five records opposite the southern edge of the Lincoln Wolds.

The plain is a large expanse of fertile loams and clay, mostly red except for a band of clay following the line of the Cotswold escarpment. In the north and north-west there are tracts of Bunter sandstones, non-calcareous rocks and sandy glacial deposits producing uplands. Much of the whole area is covered by drift deposits.

There are two plainly distinguished types of country—the heavy red pasture lands of the plain itself, and the infertile, fairly well-wooded uplands rising above it, and it is on the second of these that the wood ants are found, with three exceptions. The first is Ley Park (F) near Gloucester, and beyond the fact that the wood is of conifers no information about local conditions is available. Trench Wood (G) is less certainly on clay. According to the Ordnance Map (solid edition) it is on Lower Lias clay, but there is drift in the neighbourhood and this may extend to the wood itself, as the boundary is indefinite. No information about local conditions has been obtained. At Knowle (A) only the district is given. It appears to be sparsely wooded and quite definitely on Keuper marls, though there is some sandstone near by.

The majority of the records from the uplands are from the Bunter sand-

stone, but there are four from the Igneous and Pre-Cambrian rocks of Charnwood Forest and the Leicester coal-field, and the four Lincolnshire records are from glacial sand.

2. *The Somerset Plain and North Somerset.* This is the wide gap between the Jurassic rocks and the south-west peninsula. Most of it is low-lying pasture or arable land with heavy soil liable to flood, but in the south there is a more elevated tract of greensand producing highly calcareous soil.

As might be expected, wood ants are scarce, occurring at only two places. At Brockley (A), in North Somerset, the exact situation is not given, and there are a number of rock formations in the neighbourhood on any of which the nests may be placed. Ivythorn Wood (B) is on Lower Lias clay and Rhaetic beds, and originally consisted of larch and limes, but these have now been felled, leaving oak. Such vegetation suggests a dry soil, but no information about local soil conditions in the wood is available. The colony is small, and apparently the only one in the district.

3. *The Great Clay Vale.* This enormous tract of land stretches from South Wiltshire to Tees mouth in Yorkshire, but its northern boundary is obscured by drift deposits. It includes the Vales of Oxford, the White Horse, Aylesbury, the Bedford Ouse, Lincoln, York, and Pickering, and the Fenlands. Practically the whole expanse consists of Oxford and Kimeridge clay with Keuper marls. North of Bedford it is modified by superficial deposits of boulder clay, glacial sand and gravel, peat and alluvium, and in the same district there is a ridge of Lower Greensand, also partly obscured by drift deposits.

It is a region of damp pastures and arable land, and from the whole expanse there are only two records, neither from clay. One is from the Greensand, and the other from glacial gravel.

4. *The Lancastrian Plain.* This lies between the Lake District and the South Shropshire uplands, and includes the Cheshire Plain. With the exception of outliers from the Pennines on either side of the River Ribble, it is lowland, and the whole district has been heavily glaciated, and is covered mostly by boulder clay, but there are also large deposits of glacial sand and gravel, and smaller ones of peat and alluvium. The soil is heavy and the north and south are under permanent pasture; the middle portion, on lighter loams, is arable land.

There are only two definite records for wood ants, one from Dunham Park and one from Delamere Forest where they probably no longer exist. An observer who has lived in the district for the past thirty years has never seen them there or anywhere in the neighbourhood, though he considers the conditions to be ideal. They have been reported from the Ribble Valley and from the Leete Valley in Flintshire, but neither record has been confirmed, and the Leete Valley, on limestone, has been described as a very unlikely locality. Their occurrence in the Ribble Valley is more probable, for conditions there resemble more closely those in the valleys of the eastern Pennines, where wood

ants do occur. There the climate is drier, however, and Willoughby Gardner suggests that the scarcity of wood ants on the western side of the Plateau may partly be due to heavy rains during the breeding season.

5. *The Chalklands.* This includes Salisbury Plain, the North and South Downs, the Berkshire Downs, the Chiltern Hills, the East Anglian Chalklands, and the Lincoln and Yorkshire Wolds and as the nature of the soil is varied by local modifications such as leaching and the presence of superficial deposits, the region will be considered in four subsections.

(*a*) *Salisbury Plain, the Dorset Heights and the South Downs.* These consist of pure chalk producing bare downland with few woods, and records are consequently rare. There are three, however, from places where there are local deposits of glacial gravel and clay-with-flints, capable of supporting woodland, but in each the ants are local and scarce. In one the soil is reported to be light. A record from Affpuddle in Dorset more probably refers to the adjacent sand. From the South Downs there are three records, all indefinite. One is for the Brighton district, one for Graffham where the nests are more likely to be on the nearby Greensand, and one for Lewes where several formations approximate. Winged ants have been reported from Dover.

(*b*) *The Chalk Downs.* Reference has already been made to the Rochester district, where loam covers the chalk and wood ants are to be found. They have also been reported from Kingsgate (A) in the extreme east, but again the record is indefinite. The district is sparsely wooded, but there are patches of loam and sand which may support trees and on which the ants may be found.

(*c*) *The Marlborough Downs and the Chiltern Hills.* Here leaching has produced strips of clay-with-flints, supporting beech hangers, along the steep slopes. There are no records from the Chilterns, and two from the Marlborough Downs. Both these are on clay and in both the ants are probably now extinct.

(*d*) *East Anglia, and the Lincolnshire and Yorkshire Wolds.* Much of this region is covered by boulder clay. The soil varies, but is chiefly stiff chalky clay producing arable and pasture lands, and there are no records for wood ants. Between Cambridge and Bury St Edmunds there is a large patch of coarse sands on which wood ants are said to occur, but the record is unconfirmed.

The points gathered from the foregoing discussion may be summarized as follows: Wood ants are generally absent from fertile and heavy clay soils, and from chalk except where local modifications produce a light soil. Low-lying country appears to be avoided.

B. *Wales*

Wood ants are by no means common in Wales, but they are more frequent in the south than in the north. The records are distributed round the coast, with a few in the valleys of the central land mass. Their scarceness in North and Central Wales is no doubt largely due to the barren nature of much of the country. In South Wales they are restricted to the wooded valleys of the coal-

field area, none being reported from the Black Mountains or the south-west peninsula. They appear to be nowhere very abundant, their colonies remaining fairly constant or possibly increasing slightly. There is one record from limestone, for a wood on a slope near Castell Coch where there used to be a nest, but the wood has been felled and the ants have gone. They have been reported from Cwrt-yr-ala (A), where again they appear to be now extinct, but here it is uncertain whether they were on clay or limestone as only the district is given.

C. *Scotland*

The position in Scotland has not been considered in any great detail, but a certain amount of information may be obtained from the distribution map, and from comparisons with physical and geological maps.

The following points stand out clearly from the distribution map:

1. Wood ants are absent from the Southern Uplands and from the Central Lowlands with the exception of West Ayrshire.
2. Most of the records are from the eastern side of the country, and are inland.
3. A few records are scattered along the west coast.

Comparison with the physical map shows that the records form a fringe round the mountain mass of the Highlands, and that they are to be found in all the main river valleys. They do not occur in the mountain mass itself, and are more frequent in the Grampians than the North-western Highlands.

The Grampians and the greater part of the North western Highlands are composed of Pre-Cambrian and Igneous rocks yielding poor infertile soil. Only in the valleys can sufficient soil accumulate to support woodland, and in many of these remnants of primaeval forests persist. In the Highlands, then, the problem of the distribution of wood ants is intimately connected with the distribution of forest land, but although there are records from all the main wooded areas, and although the ants are usually present in immense numbers, they are still local.

Their absence from the eastern coastal strip and the Central Lowlands may perhaps be in part due to the industrial and agricultural activities carried on there. The poor soil of the ancient rocks gives place to rich fertile soils derived from the Old Red Sandstone, and neither this nor the mountain limestone provide particularly suitable habitats. In Western Ayrshire there is a strip of sandy soil along the coast, where wood ants are to be found in the pine woods.

On the Southern Uplands, older rocks appear again, but it is a region of moorland and hill pastures with few woods. In the western dales where woods are more frequent the ants might be expected, but none have been recorded from there. The heavy rainfall may be partly responsible for this.

The few wooded areas along the western coast, and its high rainfall probably account for the scarcity of wood ants there.

D. *Islands*

No records have been received from the Shetlands, Orkneys, Hebrides or the Scillies, from Arran or Lundy, or from Anglesey. There is a record dated 1876 for the Isle of Man, but no details are given, and the forester now in charge of the forest in the northern part has never seen this species in the island. Again, wood ants have been reported from Anglesey, but all efforts to

trace them have been fruitless. In the Isle of Wight, which continues the geological features of the mainland, they are locally fairly abundant on light soils. Of the Channel Islands, the only record is from Jersey, where in 1901 they were common near Grouville Station.

4. Factors controlling wood ant distribution

A. *Frequency tables*

To test the conclusion reached from the distribution map that certain rocks are more suitable for wood ants than others, the average number of records per 100 square miles (frequency) was calculated for each rock formation in England and Wales, and comparisons made (Table 2). The areas were deter-

Table 2

Rock formation	Symbol	Area sq. miles	Total no. of records	No. of records on several formations	No. of records on drift	Frequency No. of records per 100 sq. miles
Oligocene	i^{8-11}	139	13	4	1	9·4
Bagshot and Bracklesham Beds	i^{4-7}	722	107	11	3	14·8
London Clay	i^{3}	1246	24	8	5	1·9
Oldhaven, Reading Beds	i^{1-2}	684	11	4	1	1·6
Chalk	h^{5}	6442	14	9	1	0·2
Upper Greensand	h^{4}	389	2	1	0	0·5
Gault	h^{3}	428	0	0	0	0
Lower Greensand	h^{2}	739	21	2	0	2·8
Weald Clay	h^{1}	582	3	2	0	0·5
Hastings Beds	h	667	17	0	0	2·5
Purbeck Beds	g^{14}	3	1	1	0	33·3
Portland Beds	g^{13}	28	0	0	0	0
Kimeridge Clay	g^{12}	634	1	0	0	0·14
Corallian Beds	g^{11}	170	9	2	0	5·3
Oxford Clay	g^{10}	1436	2	2	0	0·1
Great Oolite, etc.	g^{6-8}	869	4	2	0	0·5
Inferior Oolite	g^{5}	972	17	5	0	1·7
Upper Lias	g^{3-4}	192	7	4	2	3·6
Middle Lias	g^{2}	416	0	0	0	0
Lower Lias	g^{1}	1811	7	4	0	0·4
Rhaetic Beds	fg	45	1	1	0	0·2
Keuper Red Marls	f^{6}	3096	5	5	1	0·16
Keuper Red Sandstones	f^{5}	629	1	0	0	0·2
Bunter Sandstones	f^{1-3}	1437	9	1	1	0·6
Magnesian Limestones	e^{2-4}	610	3	0	0	0·5
Permian Marls and Sandstones	e	654	0	0	0	0
Coal Measures	d^{5}	4034	18	4	2	0·5
Millstone Grit	d^{4}	2083	27	4	2	1·3
Carboniferous Limestone	d^{1-2}	3393	14	4	6	0·4
Culm Measures	d	1193	7	3	0	0·6
Devonian and Old Red Sandstone	c	3599	19	3	0	0·5
Silurian	b^{1-7}	5891	16	3	0	0·3
Cambrian	a	256	2	1	0	0·8
Pre-Cambrian	x	202	1	1	0	0·5
Granite	G	655	6	3	0	0·9

mined from the Ten Mile Geological map by means of an Amsler planimeter, but no measurement of drift-covered areas was attempted, and records from such areas are regarded as referring to the underlying rock, a procedure justified to some extent by the fact that the nature of glacial drift is frequently determined by the rock it overlies. The total number of records for each formation is shown in one column, the number actually on drift in another, and the number referring to more than one formation in a third; the two latter are included in the total, which is the figure used in calculating the frequency.

The frequency figures cover a wide range, from 14·8 (Bagshot beds) to 0·1 (Oxford Clay). The result for the Bagshot beds is exceptional, however, and a more appropriate range would be between 2·8 and 0·1. This excludes the figures for the Corallian (5·3), Oligocene (9·4) and the Purbeck beds (33·3). but all of these are disproportionately great compared with the majority which fall between 1 and 0·1. The high figure for the Purbeck beds is given by the occurrence of one record in a very small area, and as it is uncertain whether it really belongs to the Purbeck beds it is better ignored.

In Table 3 the frequency figures are shown in their appropriate soil groups (Table 1). The Upper Liassic and Oolitic rocks have been omitted because separate sets of figures for the sand and limestone regions would be necessary, and it is impossible to determine them with any degree of accuracy. However, as far as can be discovered, colonies on these rocks are on sand or thin clay.

Table 3

Sand		Non-calcareous rock		Clay		Calcareous rock		Unclassified	
i^{4-7}	14·8	d^4	1·3	i^3	1·9	e^{2-5}	0·5	g^{3-4}	3·6
i^{8-11}	9·4	G	0·9	h^1	0·5	d^{1-2}	0·4	g^5	1·7
g^{11}	5·3	a	0·8	g^1	0·4	h^5	0·2	g^{6-8}	0·5
h^2	2·8	d	0·6	fg	0·22			g^9	0
h	2·5	d^5	0·4	f^6	0·16			g^{13}	0
i^{1-2}	1·6	c	0·5	g^{12}	0·1				
f^{1-3}	0·6	x	0·5	g^{10}	0·1				
h^4	0·5	b	0·3	h^3	0				
f^5	0·2			g^2	0				
e	0								

Despite a certain amount of overlapping the frequency figures fall into three distinct groups:

Group 1. Sandy soils with frequencies greater than 1·5.

Group 2. Non-calcareous soils with frequencies between 1·5 and 0·5.

Group 3. Clay and calcareous soils with frequencies below 0·5.

In Group 1 exceptionally low figures are given by the Bunter sandstones (0·6), the Upper Greensand (0·5), the Keuper sandstones (0·2) and the Permian marls and sandstones (0), and reasons for this will be suggested later. The low figure for the Silurian rocks in Group 2 is not altogether surprising when the large area and the barren nature of much of the country is taken into account. In Group 3 a high figure is given by the London clay (1·9) and this is the most

serious aberration; but there are several modifying factors. Of its 24 records, eight may be on other formations, five more are actually on glacial gravel, and for five more only the district is given, leaving six which may definitely be said to be on London clay. These six, together with the five on drift, give a frequence figure of 0·8 which is nearer the average for Group 3. London clay varies greatly in texture, and in one of the six definite records the soil is known to be light, and in two more the clay is replaced by gravel.

It must be emphasized that in these tables the numbers of *records* for each rock has been used, and that this is no indication of the number of nests, for whereas one record may refer to a single nest, another may refer to dozens. However, with the exception of Symond's Yat, very large colonies are all reported from sand or non-calcareous rock, so no serious misrepresentation is made. It must be remembered, too, that wood ants recorded from sand and non-calcareous rock are generally to be found on those rocks, whereas records from chalk or clay are more often found to refer to sand or gravel.

B. *Records from clay and calcareous rocks*

As clay and calcareous rocks appear to be unsuitable for wood ants, all the records connected with them either theoretically or by definite report will now be examined.

1. *Records from clay.* The Gault and Middle Lias clay have no records, and the Kimeridge clay one. There are three possible records for Oxford clay, but they are all from north-east Yorkshire where it is represented by sandstone and shales. The six records from the London clay have already been mentioned and it may be repeated here that only three of them may be on heavy soil. From the Lower Lias there are two records—Ivythorn Wood, Somerset, which is also on Rhaetic beds and where the soil is probably clay, and Trench Wood (G) which may be on drift. The red Keuper marls of the Midlands and elsewhere provide five records, but only one (Ley Park) appears to be unmistakably on heavy soil. Glacial drift occurs in Sheat Hedges Wood (H) and probably in Hay Wood (I) which is shown on Keuper marls on the Ordnance Map but falls within the hypothetical drift boundaries. The other two are indefinite records—Cwrt-yr-ala (South Wales A), and Knowle (Midland A) and the last named may possibly refer to Hay Wood.

In all these places the soil is assumed to be heavy from the nature of the rock producing it, but there are three records of wood ants actually living on heavy soil. In Albyn's Covert (J) twenty years ago there was one large nest, now gone, and in Daglingworth Wood (E) two large "diseased" nests were found in 1931, but were not expected to persist. On the other hand, wood ants are abundant at Symond's Yat on heavy, clayey soil.

On the light clay at Firestone Copse, Tilsmore Wood, Felcourt Heath, Brogue's Wood and Fox's Cross, wood ants are plentiful and apparently increasing in numbers. Their local occurrence on the thin clay overlying Oolite in

Gloucestershire woods has already been mentioned. The soil here is very dry with a marked calcareous reaction except in the more exposed parts, and the ants, which are found in the open parts of the woods, do not seem to spread to any extent.

In Yorkshire the Inferior Oolite is represented by sandstone and on this the ants flourish. There are four records from the soft shales of the Upper Lias in north-east Yorkshire, but of these one may refer to the adjacent sand. In Arnecliffe Woods (Eskdale) where wood ants were reported formerly, the shales are covered by boulder clay, but as there is no trace of the ants now, it may be inferred that neither kind of clay was favourable. The other two records are from Baysdale, and Stonehouse Wood, near Whitby, where there was formerly a nest from which ants were collected for pheasants. It is possible that they were introduced for this purpose in the first place; there was no colonization and the ants have gone. A similar thing may have taken place in Arnecliffe Woods.

Summary. 1. Wet low-lying clay soils are avoided.
2. Light well-drained clays may support flourishing and increasing colonies.
3. Clay derived from Oolite may support a few colonies, but they do not appear to have spread much.

2. *Records from calcareous soils.* The results from chalk have already been discussed, and it may be repeated here that no wood ants have been proved to occur on it. The records for limestone need examination, and the Carboniferous and Permian limestones may be taken together for this.

Seventeen records have to be considered, and of these four may be dismissed at once as they are in the north of England where the limestone is replaced by sandstone. In the woods crowning Symond's Yat, Great Doward Hill and Coldwell Rocks the soil is leached, and this is very probably the case for six more records from hilly districts (L). One locality may be glaciated (M) and two more may be on other rocks (A, South Wales, Somerset).

The number of records for limestone is, therefore, certainly less than is at first apparent. It may be added that the ants are extinct in six of these places, of which four are in the West Riding where they are believed to have been introduced.

Summary. 1. There are no definite records from chalk.
2. Wood ants are uncommon on limestone, but occur on hilly ground where leaching has taken place.

C. *Soil as a limiting factor*

In attempting to explain the presence of wood ants on certain soils and their absence from others, both the physical and chemical properties of the soil must be taken into account.

(*a*) ***Physical properties.*** As the underground nest is excavated in the soil itself, the quality of this is of great importance, for if it were close and liable to

become waterlogged it would be difficult to work and aerate and after heavy rain the ants would run the risk of being drowned or suffocated. The unsuitability of heavy clays and chalk is at once apparent, for both retain water and become sticky after rain. Furthermore in dry weather clay becomes hard and cracked and chalk bakes into stony lumps, though the protecting heap of debris might to some extent prevent this happening in the underground nest. In addition, clay may be permanently deficient in air owing to its high water content.

The preference of the ants for a well-drained soil is shown by their close association with hill slopes, departed from only where the soil is sandy and therefore dry. Under these circumstances they can live equally well on low ground, as shown by the large numbers of colonies in Hampshire. This is in accord with the previously noted fact that adequately drained clay soils form quite suitable habitats. Further evidence is provided by three attempts to introduce wood ants into coverts on clay soils at Swanmore, Hants, where they are fairly abundant on the neighbouring sand. The ants flourished up to a point in dry weather but died after heavy rain. At Alderwasley (Derbyshire), too, they abound on sand but are absent from the neighbouring clay lands.

This all points to the conclusion that in the case of clay its property of retaining water renders it unsuitable for wood ants. Calcareous soils, however, are generally dry, despite their tendency towards stickiness after rain, and a further explanation must be sought.

(*b*) *Chemical constitution.* Sandy and poor siliceous soils provide the largest number of records, an overwhelming majority being from sand. Both are poor in mineral salts, especially lime, both have a marked acid reaction, and both contain peaty humus, but sand has a lower basic mineral content than siliceous soils. This is important, and suggests a possible preference for an acid soil. Most clays have an acid reaction, and mention has already been made of their suitability when drainage is assured, except in the case of those overlying Oolitic limestone. These, despite their excellent drainage, are less satisfactory, which suggests that here there is some other disturbing factor—most probably the presence of lime, a conclusion strengthened by the extraordinarily low number of records obtained from the calcareous rocks. In connexion with this evident dislike for lime it may be recalled that no ants are found on the highly calcareous Upper Greensand of East Devon, and that in the open parts of the woods on Oolitic clay where the wood ants made their nests, the soil reaction is more nearly neutral. It may also be added here that in 124 cases out of the 166 where some indication of the vegetation has been given, this is of the acid heathy type.

A further restricting factor seems to be present in red soils from which very few records have been obtained despite their large area. The poverty of the Keuper marls has already been mentioned; there is one record from the Keuper sandstones and none from the Permian sandstones, both of which invariably

form part of the infertile patches in the Midland Plain on which wood ants are to be found. Both produce light soils, and the absence of ants from them is a little surprising. The soil derived from the Devonian rocks (11–13 records) is variable, but the ants seem to be on shales and in one report the soil is said to be a yellow-red shaly clay. Rothney comments on the extreme scarcity of Hymenoptera Aculeata round Dawlish where red soil predominates. From the Old Red Sandstone there are four, possibly five, records; and Dr O. W. Richards states that in the Woolhope district wood ants are found in the Silurian rocks but never on Old Red Sandstone. The absence of ants from south-west Wales which consists largely of this rock has already been remarked.

On the whole, the evidence seems to show that red soils may contain some adverse factor. According to Lord Avebury (**3**) the presence of iron sesquioxides which are injurious to animal life is responsible for the absence of fossils from these rocks, and it may be that they are also in some way harmful to wood ants.

In connexion with soil as a factor controlling the distribution of wood ants, MacLagan's (**9**) experiments on *Smynthurus viridis* (Collembola) may be mentioned. They indicate that the rate and extent of growth, the rate of attainment of sexual maturity, and the number of eggs deposited are all affected by the nature of the soil on which the nymphs are reared. Furthermore when the females are allowed a choice of soils for oviposition, that selected by the majority is found to have a pH value of approximately 6·2. It is known that earthworms are most numerous in approximately neutral soils (even slight deviations from the optimum being injurious) and that snails with calcareous shells are restricted to alkaline soils, whereas those with hyaline shells exist over a wide range. Soil actually passes through the body in both *S. viridis* and earthworms, and the harmful effect which might be produced by one differing greatly from the internal physiological condition is easily imagined. In snails, however, the soil must act through the vegetation on which they feed, and in this way it is able to exert a considerable limiting influence on those species with calcareous shells. Wood ants are omnivorous, but depend largely for food on honey dew obtained from Aphides feeding on the surrounding trees. This honey dew is practically unchanged plant sap. Mr Elton has suggested that the preference of wood ants for acid soils may be connected with the manufacture of formic acid which is especially abundant in this species, and if this is so the influence of the soil works indirectly through the honey dew, so removing the ants one step further from the source of their acid supply.

D. *Further factors influencing distribution*

1. *Trees.* In only eight cases have nests away from trees been recorded, though they are quite often under scrub, and in three of these trees were near and were worked for food. Near Lustleigh Cleave there is a nest in a hedgerow; wood ants were previously found in a wood near by, and the present nest has probably originated from there. A large colony was found among gorse and

heather above Dean Wood, Buckfastleigh, and here the tracks of the ants extended all over the wood and also on the moors above the colony. In the hedgerows bordering two lanes near Idless, Cornwall, there are nine nests, with a further one in a hedgebank between the two lanes. In Lady's Wood, on the other side of the village, ants are plentiful, and though it is too far away to be worked by the ants in the lanes they probably originated there. In Jugger Howe Dale and on Silpho Moor, Scarborough, there are a number of nests on open moorland, but these probably spread from the adjoining Derwent Valley in the lower wooded parts of which wood ants are abundant. Elgee (**5**) mentions wood ants in Baysdale and Great Hograh, both of which are treeless. He considers the occurrence of this species in bare valleys to be an indication of the presence of trees there in the past in accordance with his view that all the moorland valleys were originally forest land. In support of this he adds that in north-east Yorkshire wood ants are only found in old woods and plantations, an opinion generally held throughout the country and supported by their liking for constructing their heaps against tree stumps.

As this species is associated so closely with woods, the felling of trees for timber affects their distribution considerably, and in many places they have disappeared as a result of this. They should be regarded as valuable members of the dry oakwood fauna because of their predilection for the larvae of *Tortrix viridana* which does immense harm to the timber.

2. *Light.* Throughout open-canopied woods the nests may be distributed evenly, but where the shade is more dense the nests are constructed in clearings, along paths and round the edges of the woods. This is strikingly illustrated in Burnham Beeches where a small patch of birchwood contains a number of scattered nests, the surrounding beechwoods having none. In the Cotswold beechwoods the nests are all in the open. However, despite this preference for light, nests are frequently almost completely covered by bracken.

3. *Game preservation.* In many parts this practice is a very powerful factor, and Stainforth considers the absence of wood ants from the East Riding to be largely due to its influence. In some places they have been introduced as food for pheasants; such are Brogues Wood, Kent, and Harleston Firs, Northants, where their numbers increased when game preservation was ceased, and diminished when it was continued. In several places where they were present formerly they have been exterminated by keepers digging up the nests for the young birds, e.g. Lady Park Wood, Durham; Stow Wood, Oxfordshire; Stonehouse and Leeshead Woods, Yorkshire. In the opinion of Mr Rosse Butterfield and Mr W. D. Roebuck, wood ants were introduced into the woods in the western part of north-west Yorkshire, where they are now practically extinct. They are said to have been introduced into Flag Quarry and Brathay Hall Woods, Windermere, for the wild pheasants, and also into Shirlett Woods, Shropshire. Large numbers are taken every year from Stoke Green, Bucks, to Windsor Forest.

Generally speaking, pheasants are not found in the woods containing wood ants, though they may be in others near at hand. Game birds are the chief enemy of this species, but green woodpeckers (*Picus viridis*) may also be responsible for a considerable amount of destruction (5).

4. *Fires.* Wood ants are particularly liable to extermination or reduction in numbers by fire on account of their preference for dry, heathy country. This has taken place at Lower Star Post, and Penny Hill, Berks, Bentley Wood, Suffolk; Farnham, Frensham Common, and Pyrford, Surrey, and in West Hampshire and East Dorset.

SUMMARY

1. Maps showing the distribution of wood ants (*Formica rufa*) in England, Wales and Scotland were prepared from data collected from various sources.

2. Wood ants are distributed throughout the whole country, but the records are concentrated in certain districts.

3. On comparison with physical and geological maps it is found that hilly country contains more records than flat, and sandy and siliceous soils more than calcareous and clay soils.

4. Tables showing the frequency with which records occur on different rock formations were prepared. The frequencies for sandy soils are considerably greater than any others; those for clay and calcareous soils are the lowest.

5. Records from clay and calcareous soils are actually fewer in number than is at first apparent.

6. It is suggested that in the case of most clays the high water content is the most important limiting factor, but the chemical constitution of calcareous and red soils is also significant.

7. Further factors influencing the distribution of wood ants are: the presence of woodland; tree felling; the intensity of light; game preservation; fires.

8. Glacial deposits (boulder clay, glacial sand and gravel) have been included in the distribution map for England and Wales.

Table 4

Rocks. The symbols are explained in Table 1. In addition the following have been used: all. = alluvium, b.cl. = boulder clay; g.g. = glacial sand or gravel; c.w.f. = clay-with-flints; L. = loam over chalk; met. = metamorphic rocks; mor. = morainic drift.

Soil. C. = clay; L. = loam; S. = sand; G. = gravel; P. = peat; c.l. = clayey loam; s. = shale; f. = flints; p.l. = peaty loam; s.l. = sandy loam.

Vegetation. A. = ash; Al. = alder; B. = birch; Be. = beech; C. = conifers; E. = elder; L. = larch; O. = oak; P. = pine; S. = spruce; S.c. = Spanish chestnut; Sy. = sycamore; b. = bramble; br. = bracken; h. = hazel; he. = heath; ho. = holly; r. = rhododendron; y. = yew.

Number. The actual number of nests is given where possible. In other cases the following symbols are used: v.n. = very numerous; n. = numerous; c. = common; f.c. = fairly common; n.c. = not common; L. = local; Sev. = several; ex. = extinct.

References. Only published records are given references, the rest being from communications, specimens or personal observation.

Table 4 (*contd.*)

* Specimens have been obtained from these localities

County	Locality	Rock	Soil	Vegetation	No.	Reference
Berkshire	Near Aldermaston Park	g.g.	S.	—	f.c.	—
	Breach Copse, Wokingham	i^6	G.	O.	n.	—
	Burghfield and Mortimer	g.g.	S.	—	f.c.	—
	Caesar's Camp, Camberley	i^6	Poor	P.	1	—
	Crowthorne	i^6	—	C.	—	28
	Kingston	g^{11}	—	O. bushes, C.	—	59
	Lower Star Post, Camberley	i^6	Poor	B. scrub, he.	c., ex.	—
	Palmer's Lake Wood, Wokingham	i^6	G.	P., B.	n.	—
	*Penny Hill, Camberley	i^6	Poor	B. scrub, he.	5	—
	Tubney Wood	g^{11}	S.	B., P., O., Sy.	6	—
	Wellington College	i^3	—	—	—	24
	Windsor Forest	i^3, i^4	—	—	—	—
Brecon	Ystradfellte	d^4, b.cl., g.g.	—	—	—	31
Buckinghamshire	*Burnham Beeches	g.g.	S.	B., ho., he., br.	c.	—
	*Stoke Green	g.g.	G.	P., Be., O.	n.	—
Cambridgeshire	White Wood, Gamlingay	h^2	—	—	—	—
Carnarvonshire	Llanberis	b; a	—	—	—	21
Cheshire	Delamere Forest	g.g., f^4	—	—	? ex.	35
	Dunham Park	b.cl.	—	—	—	35
Cornwall	*Bishop's Wood, Idless	C	c.l. light	O., b.	7	10
	*Blackadown, Idless	C	c.l. light	h., b., ho.	4	—
	Shortlanesend, Idless	C	c.l. light	h., b., ho.	5	—
	Trenowth Wood, Grampound Rd.	C	c.l.	O. scrub	L.	—
Cumberland	Ashness Wood, Keswick	b^2	S.	C., O., scrub	v.n.	—
	Bassenthwaite	b^2	—	—	—	—
	Parkhead, Caldbeck	d^2, d^3	S.	O.	v.n.	—
Denbigh	Crotnant	b	—	—	—	25
	Deganwy	b	—	—	—	25
Derbyshire	Ambergate	d^4	S.	L. mixed	v.n.	—
	*Birch Wood, Cromford	d^4	S.	L. mixed	n.	—
	Cromford	d^4	S.	—	—	—
	Little Eaton	d^4	S.	—	—	40
	*Long Way (Wirksworth)	d^4	S.	L. mixed	n.	—
	*Longshore Wood	d^4	P.	B., P., O., br.	v.n.	—
	*Peat Pills Wood, Alderwasley	d^4	S.	L. mixed	v.n.	—
Devonshire	Bickleigh Vale	C	—	—	—	—
	Bovey Tracey	i^{12}	S.	—	n.	—
	*Bridford Wood	d	S.	O.	50	—
	Buckfastleigh	C	S.	—	n.	—
	*Cannon Teign Wood, Ashton	d	Light	O., S., ho.	1	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Devonshire	Clifford Bridge	d	—	O. and Al. scrub	12	—
	Dawlish	—	—	—	—	45
	Dean Wood, Buckfastleigh	C	C. light	O., Be., he.	v.n.	—
	Fordlands, Exeter	d	—	—	—	—
	Gidleigh Park	G	—	O.	1	—
	Haldon Moor	i	Poor	Be., C.	n.	—
	Holne Bridge	d, c^3	Thin	Be., O.C.	n.	—
	King's Wood, Buckfastleigh	c	S.	O. scrub, C.	v.n.	—
	Kingsteignton	i^{12}	—	—	—	—
	*Lustleigh	G, d	Light	Near O, P, h.	1	—
	Marsh Mills	C	—	—	—	—
	Shaughbridge	C, g.g.	—	—	—	—
	Virtuous Lady Mine	C	—	—	—	18
	Webburn Valley	G, d	G	O. dwarf	9	—
Dorset	Affpuddle	i^2, h^5	—	C.	c.	—
	Bere Heath	i^4	—	Mixed	c.	—
	Bloxworth	i^2, i^3	—	Mixed	c.	—
	Bloxworth Heath	i^4	—	Mixed	c.	—
	Broadstone Common	i^4	S. or P.	C.	2	—
	Bushey	i^4	S.	O., P.	c.	—
	*Cannon Hill, Wimborne	i^4	P.G.	P.	Under 20	—
	Clyffe	i^2, g.g.	—	—	c.	—
	Coombe Heath	i^4	—	Mixed	c.	—
	Coombe Keynes	i^3	—	Mixed	c.	—
	Coombe Wood	i^2	—	Mixed	c.	—
	Corfe	h^2, i^4	—	—	c.	—
	Dudsbury	i^4, i^5	—	O.	c.	—
	East Stoke	i^4	—	P.	c.	—
	Galton	i^2	—	P.	c.	—
	Grange Woods	i^4	—	P. or mixed	c.	—
	Godlingstone Heath	i^4	—	P., O.	c.	—
	Highwood Heath	i^4	—	Mixed	c.	—
	Holme Heath	i^4	—	P.	c.	—
	Holnest	g^{12}	—	—	—	—
	Hyde	i^4	—	P.	c.	—
	Hyde Heath	i^7	—	P.	c.	—
	Lulworth Cove	g^{14}, h^1, h^4	—	—	n.	37
	Middlebere Heath	i^4	—	P., O.	c.	—
	*Morden	i^4	—	P.	n.	—
	Moreton	i^4	—	P., r.	c.	—
	Newton Heath	i^4	—	P., O.	c.	—
	Owermoigne Heath	i^4	—	P.	c.	—
	Parley Heath	i^4	—	—	c.	—
	Povington Heath	i^4	—	P.	c.	—
	Puddleton Heath	i^2	—	P.	c.	—
	Redbridge	i^5, g.g.	—	P., S.c.	n.	—
	Rempstone Heath	i^4	—	P., O.	c.	—
	Sand Banks, Poole	i^4	S.	—	c.	—
	Slepe Heath	i^4	—	P., O.	c.	—
	Stoborough Heath	i^4	—	P., O.	c.	—
	Studland Heath	i^4	—	P., O.	c.	—
	Upper Rockhampton	i^2	—	—	c.	—
	Warmwell	i^4	—	P.	c.	—
	West Knighton Heath	i^4	—	P.	c.	—
	Woodsford	i^4	—	P.	c.	—
	Wool Barrow	i^4	—	Mixed	c.	—
	Wool Heath	i^4	—	P.	c.	—
	Wytch Heath	i^4	—	P., O.	c.	—
	Yellowham Heath	i^2	—	—	c.	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Durham	Chopwell Woods	b.cl., g.g.	—	C.	v.n.	—
	Gibside	d^5	—	—	1	—
	Howgill	d^5, b.cl.	Boggy P.	S., Al.	50	—
	Lady Park Wood, Gateshead	d^5	—	—	ex.	—
	Shotley Bridge	d^4	—	—	1	—
	Staindrop	b.cl.	—	—	—	36
	Winlaton	b.cl., d^5	—	—	—	16
Essex	Bassett's Wood, Little Baddow	i^3, g.g.	—	—	—	—
	Billericay	i^3, i^4	—	—	—	—
	Birdbrook	b.cl.	—	—	—	28
	*Chantry Wood, Wickham Bishops	i^3	c.l., G.	O., A., h., br.	30	—
	High Woods, Colchester	i^3	—	—	v.n.	—
	Hockley	i^3, i^4	—	—	2	—
	Lingwood Common	g.g., l.	—	—	—	—
	*Sparkey Wood, Wickham Bishops	i^3	c.l., G.	O., h., A.	—	—
	Woodham Walter Common	g.g., i^3	—	O. scrub, B.	12	—
Glamorgan	Briton Ferry	d^5, b.cl.	—	—	—	25
	*Brynau Valley, Castell Coch	d^4	—	br.	n.	—
	Castell Coch	d^2	—	—	ex.	—
	Cwrt-yr-ala	f^6, d^2	—	—	ex.?	—
	Pontneath-Vaughan	b.cl., d^5	—	—	—	57
Gloucestershire	Chalford	g^5	—	—	—	60
	Cirencester Park	g^7, g^8	—	—	v.n.	—
	Coldwell Rocks	d^2	—	—	v.n.	60
	*Dark Wood, Woodchester	g^5	C. light	Be.	11	—
	Dean Forest	d^5	—	Be., Ho.	—	30
	Great Doward Hill	d^2	—	—	—	56
	Gorsley	c, b^{6-7}	—	—	—	—
	Ley Park, Westbury	f^6	—	c.	—	—
	Mitcheldean Rd. Station	—	—	—	n.	—
	*Newent Woods	c	—	Be., L.	v.n.	—
	Overley Wood, Daglingworth	g^7	C. heavy	Be.	2	—
	Queens Wood, Much Marcle	b.	—	—	—	—
	Sapperton	g^5	Flagstones	Be.	1	—
	*Sheepscombe	g^5	—	L.	c.	—
	Slad Valley	g^5	—	—	—	60
	Stinchcombe Hill	g^5	—	—	Sev.	53
	Symonds Yat	d^2	Heavy C.	—	v.n.	—
	Ullen Wood, Birdlip	g^5	Thin	Be., L.	4 or 5, ex.	—
	Woodchester Park	g^5, g^4, g^6	C. light	Be.	—	60
	Wotton-under-Edge	g^5	—	—	—	—
Hampshire	*Amberwood, New Forest	i^5	—	O.	n.	—
	Anderwood, New Forest	i^7	—	—	n.	—
	Avon Heath	i^5, g.g.	—	—	—	—
	Biddenfield, Swanmore	i^5	Light S.	—	n.	—
	Bolderwood	i^7, i^6, i^8	—	—	n.	—
	Bournemouth	i^4	S.	P.	n.	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Hampshire	Brockenhurst	i^8	—	—	n.	—
	Broomy	i^5, i^6	—	—	n.	—
	Burley	i^6	—	—	n.	—
	College Woods, West End	i^5	—	P.	c.	—
	Denny, New Forest	i^8, i^7	—	—	n.	—
	Dimmock's Moor, Swanmore	i^5	Light	—	n.	—
	Durford Wood, Petersfield	h^2	—	—	—	—
	Eastleigh	i^5	—	—	—	—
	Farnborough	i^5, i^7	S.	—	c.	—
	Firestone Copse, I. of W.	i^{10}, i^9	C.	P., O.	c.	—
	Fleet	i^5, i^6	S.	—	c.	—
	Godshill, New Forest	i^4, g.g.	—	—	n.	—
	Harewood Forest	c.w.f., g.g., h^5	—	—	Few L.	—
	Harting Combe, Petersfield	h^2	—	—	—	—
	Hartley Wintney	i^5	—	S.	v.n.	—
	Hasley, New Forest	i^5	—	—	n.	—
	Hawley	i^5, i^7	—	S.C.	—	—
	*Headley	h^2	S.	P., O.	2	—
	Highland Water, New Forest	i^6, i^7	—	—	n.	—
	Holiday Hill, New Forest	i^7	—	—	—	27
	Holmhill, New Forest	i^6, i^7	—	—	n.	—
	Holmsley	i^8, g.g.	—	—	n.	—
	Hurn	i^5	—	—	—	—
	Island Thorns, New Forest	i^5	—	O.	1	—
	Knightwood, New Forest	i^7	—	—	n.	—
	*Lady Cross, New Forest	g.g.	—	O., P.	n.	—
	Liberties, Swanmore	i^5	Light S.	—	n.	—
	*Little Linford	i^4	—	P., O.	n.	—
	Lyndhurst	i^7	S. pit	—	—	29
	Mark Ash, New Forest	i^7	—	—	v.n.	—
	Marlboro' Deeps, New Forest	i^{8-11}	—	P.	—	—
	Matchams, Ringwood	i^5	—	—	—	—
	*Milkham, New Forest	i^6	—	—	n.	—
	Minstead	i^6	—	—	v.n.	—
	Norton, I. of W.	i^8	—	—	—	—
	Oakley, New Forest	i^6, i^7	—	—	n.	—
	Pamber Forest	i^4	Light S.	P., O., h.	—	—
	Parkhurst Forest, I. of W.	i^{10}	—	—	—	—
	Picket Hill, Ringwood	i^6, i^7	—	B., b., he., br.	12 ex.	—
	Quab, Swanmore	i^5	Light S.	—	n.	—
	Ramnor Enclosure, New Forest	i^8	—	—	—	29
	Rhinefield	i^7	—	O.	—	—
	*Roe Wood, New Forest	i^6	—	O.	n.	—
	St Leonards	i^4	—	—	—	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Hampshire	Sandy Balls Wood, Fordingbridge	i^4	S., C., G.	P.	v.n.	—
	Sloden, New Forest	i^5	—	—	n.	—
	Sopley Heath	i^5, g.g.	—	—	—	—
	Spring Woods, Basingstoke	h^5, g.g.	Light	—	n.c.	—
	Southampton	i^5, i^4	—	—	—	17
	*Talbot Wood, Bournemouth	i^4	G.	S.	2	—
	Tunworth	h^5, g.g., c.w.f.	—	O.	n.c.	—
	Ventnor	h^2	—	—	—	44
	*West Moors, New Forest	All	—	O.	—	—
	Wilverley, New Forest	i^7, i^8, g.g.	—	—	n.	—
	Wolmer Forest	h^2	—	—	—	—
Herefordshire	Hollybush Hill	a	Light c.l.	A., br., E.	3	—
	Leominster	c	—	—	—	28
	Woolhope	b	—	—	—	—
Kent	Bedgebury Park, Goudhurst	h	S.	O., S.c., P.	Sev.	—
	Blean Wood	i^3	—	—	v.n.	17
	Bredhurst	L	—	—	—	52
	*British Camp, Oldbury	h^2	S., humus	B., O., P., br., he.	L.	—
	*Brogues Wood, Biddenden	h	C.	P., O., he.	n.	—
	Chattenden	i^3	—	—	n.c.	—
	Chiddingstone	h	—	he.	c.	—
	Cooper's Wood, Canterbury	i^1, g.g.	—	—	—	60
	*Darenth Wood	i^5	S.	—	—	20
	Denge Wood, Canterbury	h^5, L. c.w.f.	—	—	f.c.	—
	*Fox's Cross, Whitstable	i^3	C. light	O. and B.	5 or 6	—
	*Goddard's Green, Benenden	h	S.	P.	—	—
	Hempstead Woods	L	—	—	—	—
	Herne Bay	i^3	—	—	—	28
	Huntingfield	L.	—	—	1	52
	Joyden's Wood, Bexley Heath	i^1, i^2	S.	O., b., h.	1	—
	Kingsgate	h^5, i^1, L.	—	—	—	28
	Maidstone	h^2	—	—	—	52
	Rainham Park	h^5	L.	—	n.c.	—
	Raspit Hill, Oldbury	h^2	S. peat	B.	v.n.	—
	Seal Chart, Oldbury	h^2	—	—	—	—
	Sheppey Cliffs	i^4	—	—	—	28
	Throwley	h^5	—	—	—	52
	Walderslade Road, Rochester	L	—	—	n.c.	—
	Wigmore, Rochester	L	—	—	n.c.	—
	Yelsted Woods	L	—	—	n.c.	—
Lancashire	*Brathay Hall Wood	b	—	O.	n.	—
	Carnforth	b.cl., g.g.	—	—	—	—
	Duddon Valley	b	—	—	—	—
	Eggerslock Wood, Grange-over-sands	d^2	—	y., h.	v.n.	54
	*Flag Quarry Woods, Windermere	b	Light	O., L.	—	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Lancashire	Holker Hall	b, d^3	—	—	—	—
	Satterthwaite	b	Wet	Hardwoods	1, ex.	—
	Silverdale	d^2	—	P., L., O.	n.	—
	Warton Woods	d^{2-3} (?)	—	—	—	—
Leicestershire	Buddon Wood	G	Humus	O., B.	12	27
	Out Wood, Charnwood Forest	A	—	—	1 ex.	46
	Sheat Hedges Wood, Charnwood Forest	f^6, b.cl.	—	—	1 ex.	46
Lincolnshire	Doddington Wood	g	G.	O., C.	6	—
	Skellingthorpe	g	G.	—	—	43
	Troy Wood, Horncastle Spa	g.g.	—	—	—	—
Merioneth	Barmouth	b	—	—	—	—
Middlesex	Enfield	i^3, g.g.	—	—	—	19
	Hampstead	i^4	S.	C.	ex.	39
	Highgate	i^4	—	—	ex.	39
	Wanstead	i^3	—	—	—	—
Monmouth	Penhow	c	—	—	—	—
	Trelleck	c	—	S.	v.n.	—
Northants	*Fox Cover, Harlestone	g^5	Poor	Mixed	—	—
	Harlestone Firs	g^5	Poor	P., he., br.	v.n.	—
	Helpstone Heath	g^7, g^5	—	—	—	—
	Thornhaugh	g^3, g^5	—	—	—	—
Northumberland	Broomley	d^4	—	P.	f.c.	—
	Corbridge	d^4, b.cl.	—	—	v.n.	—
	Devil's Water, Dipton	b.cl.	—	—	v.n.	—
	Dilston	b.cl., g.g.	—	—	f.c.	—
	Dipton Mill	d^6, d^7	—	C. mixed	f.c.	—
	Dipton Wood	d^4, b.cl.	S.f.	P.	v.n.	—
	Harbottle	b.cl., g.g.	—	—	—	—
	Holystone	b.cl.	—	—	—	—
	Lemmington Wood	b.cl., d^1	S.L.	B., P., Be., O., r.	—	—
	Morpeth	d^6	—	C. mixed	v.n.	—
	Riding Mill, Hexham	g.g.	S.	F.	F.	38
	Slaley	b.cl.	S.	P.	f.c.	—
	Styford	d^7, g.g.	—	C.	—	—
	Swallowship, Dipton	b.cl.	—	C.	—	—
	Whitley	b.cl.	—	—	n.c.	—
	Yardhope	b.cl., d^{1-2}	—	—	—	—
Nottinghamshire	Sherwood Forest	f^2	—	—	—	—
	Thorney Wood	g.g.	—	P.	—	—
	*Wigsley Wood	g.g.	S.	O., B., P.	Under 12	—
Oxfordshire	Caversham	h^5, g.g.	S.	—	ex.	—
	Stow Wood, Elsfield	g^{11}	—	B., O.	ex.	—
Shropshire	Albyn's Covert, Bridgenorth	c	C. heavy	B., h., br.	1 ex.	—
	Farley Common	b	—	—	—	—
	Shirlett, Broseley	d^5	P., S.	Mixed C.	f.n.	—
	Spring Coppice, Lyth Hill	g.g.	S.	O.	n.	—
Somerset	Brockley	d^2	—	—	L.	—
	Horner Wood, Porlock	C	—	P.	v.n.	12
	*Ivythorn Wood, Street	g^1, fg.	—	O., P.	3	—
	Minehead	C	—	—	—	—
Staffordshire	Bishop Wood, Eccleshall	f^2	—	O., L.	1	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Staffordshire	Burnt Wood	f^2	—	—	—	—
	Cannock Chase	f^2, d^5	—	—	—	—
	Hopwas Wood	f^2	L.	C.	—	—
	Idlerocks Estate, Moddershall	f^2	—	—	—	—
Suffolk	Assington Thicks	b.cl.	Poor	O., B., h., P.	2	—
	Bentley Wood	b.cl.	—	P.	f.n., ex.	—
	Holbrook Park	g.g.	—	—	—	—
Surrey	Ashstead	i^3	—	—	—	14
	Bagshot	i^6	—	—	Sev.	—
	Blackheath	h^2	—	—	—	—
	Byfleet	g.g.	—	—	—	—
	Catford	i^3	—	—	—	—
	Chobham	i^5, i^6	—	—	—	—
	*Esher Common	i^4	S.	P.	f.c.	—
	Farnham	h^2	—	P.	—	28
	Guildford	h^5	—	—	—	—
	Horsell	i^4	—	—	—	28
	*Jumps Estate, Farnham	h^2	S.	P.	1 ex.	—
	Limpsfield	h^2	—	—	—	14
	Long Cross	i^4, i^5	—	—	—	49
	*Milford	h^2	—	P.	—	—
	Oxshott	i^4	—	P.	f.c.	—
	Pyrford	i^4	—	—	—	24
	St George's Hill	i^5	—	—	—	21
	Shere	h^2	—	—	—	17
	*Thursley Common	h^2	S.	P.	4	—
	Weybridge Heath	i^4	—	—	1	21
	Woking	i^4	—	—	—	29
Sussex	Abbot's Wood, Eastbourne	h^1	—	O., C.	c.	32
	Ashling Wood	i^3	—	O.	—	—
	Balcombe Forest	h	—	P.	f.c.	—
	Bolney Woods	h (?)	—	—	—	—
	Brighton District	h^5	—	—	c.	50
	Broadstone Wood, W. Hoathly	h	—	—	—	—
	*Champs, Coldwaltham	h^2	S.	P.	1	—
	Coates, Fittleworth	h^2	S., P.	P., B.	3	—
	Creep Wood, Battle	h	S.	P.	20	—
	Crowborough Warren	h	—	—	—	—
	Eridge Forest	h (?)	—	—	—	—
	*Felcourt Heath	h	P., C.	B., Be., O., br.	2	—
	Graffham	h^5, h^2	—	—	—	13
	Guestling Wood	h	—	—	C.	—
	Heatherden Wood, Cross-in-hand	h	—	—	n.c.	—
	Hindleap Warren, W. Hoathly	h	—	—	—	—
	High Woods, Bexhill	h	—	—	—	25
	Horncastle Wood, W. Hoathly	h	—	—	C.	—
	Lewes	h^1	—	—	—	—
	Midhurst	h^3	—	C.	—	—
	Priestridge Warren, W. Hoathly	h	—	—	—	—
	St Helen's Wood, Hastings	h	—	—	C.	—
	Tilgate Forest	h	—	P.	f.c.	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Sussex	Tilsmore Wood, Cross-in-hand	h	P., C., S.	P.	n.	—
	Vetching Wood	h (?)	—	—	—	—
	Worth Forest	h	—	P.	f.c.	—
	Wych Cross Place, W. Hoathly	h	—	—	ex.	—
Warwickshire	Hay Wood, Knowle	f^6	—	—	—	22
	Knowle	f^6, g^1	—	—	—	42
	Sutton Coldfield	f^2	S.	B., O., he., br.	—	—
Westmoreland	Arnside	d^2	—	—	—	—
	Low Wood	b	—	—	—	25
Wiltshire	Rabley Wood, Marlborough	h^5, c.w.f.	—	—	c.	—
	Selwood Forest	h^4	—	S.	2	—
	West Wood, Marlborough	h^5, c.w.f.	—	—	ex.?	—
	Whetham	g^{11}	—	—	ex.?	—
Worcestershire	Bewdley	d^5	—	—	—	—
	Shrawley	f^5	—	—	—	34
	Trench Woods	g^1	—	—	—	34
	Wyre Forest	d^5	S.	O., B.	v.n.	—
Yorkshire	Arnecliffe Woods, Glaisdale	g^3, b.cl.	—	P.	ex.?	51
	Baysdale	g^3	—	he.	—	—
	Barnscliffe Woods, Langdale End	g^5, g^{10}	C.	O., P.	n.	—
	Blackhills, Wilsden	d^4	P.	P., B., he.	f.c., ex.	—
	Bloody Beck, Langdale End	g^5	C., P.	he., br.	—	—
	Bradfield	d^4	—	P.	Sev.	41
	Brockodale Woods, Wentbridge	e^2	—	—	—	—
	Crimsworth Dene, Hebden Bridge	d^4	—	—	Sev.	—
	Dalby Valley	g^{11}	S.	C.	—	—
	Denby Dale	d^5	—	P.	C.	—
	Duncombe Park, Helmsley	g^5	Light	P.	f.c.	—
	Eagle Hall Grounds, Pateley Bridge	d^4	—	—	ex.?	—
	Farndale	g^5, g^3, g^1	—	—	—	—
	Goitstock, Bingley	d^4	—	Mixed	n., ex.	—
	Grass Low Wood, Grassington	d^2	—	—	ex.	—
	Great Hograh, Commondale	—	—	O., B., he.	n.	—
	Hardcastle Crags, Hebden Bridge	d^4	—	—	C.	—
	Hebden Bridge	d^4	—	—	v.n.	—
	Honley	d^4	—	—	—	—
	Jugger Howe Dale, Langdale End	g^5	C.	he.	—	—
	Kirkstall Woods	d^4	—	—	—	—
	Leeshead Wood, Littlebeck	b.cl.	C., light	B., O.	1, ex.	—
	Levisham Woods	g^{11}	—	—	—	—
	*Newton Dale	g^{11}	—	P.	—	—
	Pickingill, Ripon	—	—	—	—	—
	Ravensgill, Pateley Bridge	d^4	—	—	ex.	—
	Riccal Dale	g^{11}, g^{10}	Light	P.	n.	—
	Silpho Moor	g^{11}	—	he., P.	n.	—

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Yorkshire	Stonehouse Wood, Littlebeck	g^3	Light clay	Be., O., L.	1, ex.	—
	Sprotboro' Woods	e^{2-4}	—	—	—	—
	Wakefield District	d^5	—	—	ex.	—
	Weldon Wood, Fryaton	e^2	—	—	—	—
	West Ayton	g^{11}, g.g.	—	—	—	—
	Wharncliffe Crags	d^5	—	—	—	—
SCOTLAND:						
Aberdeenshire	*Bannockbuie Forest, Balmoral	g.g.	Thin humus	P., S., L.	v.n.	—
	Braemar	b.cl., g.s.	—	—	—	19
	Brig of Gairn	—	—	—	—	31
	Craig Gowan, Balmoral	x	Thin humus	P., S., L.	v.n.	—
	Garmaddie, Balmoral	g.s.	Thin humus	P., S., L.	v.n.	—
Ayrshire	Barrhill	b.cl.	—	P.	—	11
	Fusherton Wood, Dunure	B	P., dark	L.S.	3 or 4	—
	Kilmarnock	—	—	—	—	11
	Mauchlin	e	—	—	—	11
	Mochrum Wood	c	—	—	—	11
	Water of Girvan	d.c.	—	—	—	11
Argyllshire	Armidale Wharf	all., met.	p.l.	B., h.	v.n.	—
	Colintraive	met.	—	P.	f.c.	—
	Loch Awe	met.	—	—	—	—
	Loch Tyne	F	—	O.	—	—
	Loch Sween	met.	—	B.	—	—
	Strontian	—	—	—	—	—
	Tighnabruaich	met.	—	P.	f.c.	—
Elgin	Logie	g.g.	—	—	—	—
Inverness	Aviemore	S, G	—	—	—	30
	Forest of Glenmore	b.cl., met.	—	—	n.	—
	Nethy Bridge	S, G	S. or G., humus	P.	v.n.	—
	Rothiemurchus	G	—	P.	v.n.	—
	Strathglass	met., mor.	—	P., B.	n.	—
Kinross	Blair Adam Estate	B	—	—	—	—
	Cleish Castle Woods	A	—	—	—	—
Nairn	*Collyuish Wood, Dunphail	—	Mossy	P.	v.n.	—
	Dulsie Wood, Dunphail	g.s. and g.g.	Mossy	P.	v.n.	—
	Greystone Wood, Dunphail	b.cl.	Mossy	P.	v.n.	—
	Shaw Wood, Dunphail	b.cl.	Mossy	P.	v.n.	—
Perthshire	Aberfoyle	met, c	—	—	—	33
	Abernethy Forest	S, G	—	—	—	—
	Black Wood, Rannoch	mor.	—	—	—	23
	Brig o' Turk	met.	—	—	—	33
	Cambusmore	c, all.	—	—	—	33
	Carie Glen, Killin	met., mor.	—	—	n.	—
	Chuallaich	met., b.cl.	—	—	—	—
	Coninish Glen	met.	—	P., br.	21	—
	Glen Suie	met.	—	—	—	59
	Loch Ard	met.	—	—	—	33
	Loch Tummel	mor., b.cl.	—	—	—	59
	Pass of Leny	met.	—	—	—	33
	St Filans	met.	—	—	c.	—
	Trossachs	met.	—	—	c.	33

Table 4 (*contd.*)

County	Locality	Rock	Soil	Vegetation	No.	Reference
Renfrewshire	Paisley	d^{1-2}	—	—	—	14
Ross-shire	*Corrie Valighan	—	—	B.	12	—
	Garve	met., mor.	—	—	v n.	—
	*Guchbae, Garve	b.cl.	—	B.scrub	v.n.	—
	Loch Scalpey	G	—	B.	3	—
Stirling	Rowardennan	met.	—	P.	f.c.	—
Sutherland	Inveran	mor.	—	B.	n.	55
	Invershin	mor.	—	B.	n.	55
	Loch Shin	—	—	—	—	26

REFERENCES

(*a*) *General* (*in Text*)

1. **Anderson, M. L. (1932).** "The natural woodlands of Britain and Ireland." Oxford.
2. **Armitage, E. (1914).** J. Ecol. 2: 98.
3. **Avebury, Lord (1902).** "The scenery of England." London. Chap. 1.
4. **Donisthorpe, H. St J. K. (1915).** "British Ants." Plymouth.
5. **Elgee, F. (1912).** "The moorlands of north-eastern Yorkshire." London.
6. **Elton, C. (1932).** J. Anim. Ecol. 1: 69.
7. **Geikie, J. (1905).** "Structural and field geology." Edinburgh.
8. **Harmer, F. W. (1928).** Proc. Yorks. Geol. Soc. 21: 79.
9. **MacLagan, S. (1933).** Proc. R. Phys. Soc. Edinb. 22: 107.
10. **Moss, C. E., Rankin, W. M. & Tansley, A. G. (1910).** New Phytol. 9: 113.
11. **Robinson, G. W. (1932).** "Soils, their origin, constitution and classification." London.
12. **Stamp, L. D. & Beaver, S. H. (1933).** "The British Isles." London, Chaps. 2, 3, 6, 8, 11, 12.
13. **Tansley, A. G. & Adamson, R. S. (1913).** J. Ecol. 1: 81–9.
14. **Salisbury, E. J. & Tansley, A. G. (1921).** J. Ecol. 9: 19.
15. **Watson, J. A. S. & More, J. A. (1933).** "Agriculture," pp. 1–22. Edinburgh.
16. **Wilcox, H. A. (1933).** "The woodlands and marshlands of England." Liverpool.

(*b*) *Distribution records* (*Table* 4)

1. **Bagnall, R. B.** [*sic* = **S.**] **(1906).** Ent. Rec. 18: 159.
2. **Bignell, G. C. (1897).** Ent. Mon. Mag. 33: 141.
3. **Bold, T. J. (1870).** Trans. Nat. Hist. Soc. Northumb. 3: 142.
4. **Bowman (1889).** Science Gossip: 200.
5. **Box, H. E. (1917).** Ent. Mon. Mag. 53: 110.
6. **Brown, J. M. (1933).** Naturalist, Lond.: 235.
7. **Butterfield, R. & Fordham, W. J. (1930).** Naturalist, Lond.: 246.
8. **Chitty, A. J. (1901).** Ent. Rec. 13: 250.
9. **Clark, J. (1906).** Rep. R. Cornwall Polyt. Soc. 74: 96.
10. **Clark, J. (1906).** "Victoria County History of Cornwall." London.
11. **Clark, J. (1910).** Ann. Kilmarnock Rambl. Soc., 6: 38–66.
12. **Crawley, W. C. (1917).** Proc. Somerset. Nat. Hist. Soc. 62: 153.
13. **Crawley, W. C. (1918).** Ent. Rec. 30: 188.
14. **Donisthorpe, H. St J. K. (1905).** Rep. Lancs. Chesh. Ent. Soc. 29: 37.
15. **Donisthorpe, H. St J. K. (1907).** Ent. Rec. 19: 7.
16. **Donisthorpe, H. St J. K. (1908).** Zoologist, 12: 421–3.
17. **Donisthorpe, H. St J. K. (1908).** Trans. Leics. Lit. Phil. Soc. 12: 226.
18. **Donisthorpe, H. St J. K. (1910).** Ent. Rec. 22: 16.

19, 20. Donisthorpe, H. St J. K. (1911). Ent. Rec. 23: 11 & 61–2.

21. Donisthorpe, H. St J. K. (1913). Ent. Rec. 25: 89–90.

22–26. **Donisthorpe, H. St J. K. (1915).** "British ants," pp. 248, 252, 256, 265, 267.
27. **Donisthorpe, H. St J. K. (1919).** Ent. Rec. 31: 21–2.
28. **Donisthorpe, H. St J. K. (1919).** Ent. Rec. 31: 217.
29. **Donisthorpe, H. St J. K. (1923).** Ent. Rec. 35: 7.
30. **Donisthorpe, H. St J. K. (1924).** Ent. Rec. 36: 52.
31. **Donisthorpe, H. St J. K. (1924).** Ent. Rec. 36: 52, 135.
32. **Donisthorpe, H. St J. K. (1925).** Ent. Rec. 37: 3.
33. **Evans, W. (1912).** Scot. Nat.: 104–6.
34. **Fletcher, J. E. & Martineau, A. H. (1901).** "Victoria County History of Worcestershire." London.
35. **Gardner, Willoughby (1901).** Trans. L'pool. Biol. Soc. 15: 371.
36. **Harrison, J. W. H. (1927).** Vasculum, 13: 157.
37. **Hogan, A. R. (1859).** Nat. Hist. Rev. 6: 109.
38. **Hull, J. E. (1922).** Vasculum, 8: 129.
39. **Janson, E. W. (1858).** Ent. Annual: 78–84.
40. **Jourdain, F. C. R. (1905).** "Victoria County History of Derbyshire." London.
41. **Joy, N. H. (1908).** Ent. Rec. 20: 19.
42. **Martineau, A. H. (1904).** "Victoria County History of Warwickshire." London.
43. **Matthews, H. S. R. (1884).** Ent. Mon. Mag. 20: 209.
44. **Morey, F. (1909).** "A guide to the natural history of the Isle of Wight." Newport I. of W. and London, p. 302.
45. **Parfitt, E. (1880).** Rep. Devon. Ass. Adv. Sci. 12: 513.
46. **Plant, J. (1844).** Zoologist, 2: 473.
47. **Rothney, G. A. J. (1891).** Ent. Mon. Mag. 27: 78.
48. **Rothney, G. A. J. (1906).** Ent. Mon. Mag. 42: 257.
49. **Saunders, E. (1896).** Ent. Mon. Mag. 32: 161.
50. **Saunders, E. (1905).** "Victoria County History of Sussex." London.
51. **Sewell, J. T. (1917).** Naturalist, Lond.: 158.
52. **Sladen, F. W. L. (1908).** "Victoria County History of Kent." London.
53. **Smallcombe, W. A. (1914).** Proc. Bristol Nat. Soc. 4: 78.
54. **Standen, R. (1909).** Lancs. Nat. 2: 190.
55. **Theobold, F. V. (1921).** Entomologist, 54: 233.
56. **Tomlin, J. R. le B. (1910).** Ent. Rec. 22: 189.
57. **Tomlin, J. R. le B. (1916).** Ent. Rec. 28: 256.
58. **Warner, W. H. (1871).** Science Gossip: 198.
59. **White, F. Buchanan (1872).** Scot. Nat. 1: 260.
60. **White, W. Farren (1892).** In C. A. Witchell & W. B. Strugnell, "The fauna and flora of Gloucestershire." Stroud, p. 182.

SOME NOTES ON THE PLANKTON OF THE THAMES ESTUARY

By A. LAURENCE WELLS

CONTENTS

1. Introduction

The precise limits of the estuary of the River Thames are not easy to define. The Thames Conservancy's eastern limit (Crowstone to Yantlet) is generally acknowledged as forming the end of the river itself, although, geographically and physically, the head of Sea Reach makes a more satisfactory boundary. The western limit, however, is the subject of some controversy. The jurisdiction of the Port of London Authority extends to the meridian of Havengore Creek and for Custom's purposes the Estuary extends to a line drawn from Reculver Towers on the Kent coast to a point just below Clacton-on-Sea on the Essex side. A glance at the chart of the area in question (Fig. 1) will show that the typical estuarine sandbanks continue some miles farther eastward. For this reason, doubtless, Captain Tizard, R.N. in his Hydrographical Surveys in the *Triton*, 1882–9, gives the eastern boundary as being a line from the North Foreland, Kent, to Harwich, Essex, via the Kentish Knock Lightvessel (Fig. 2). The "Company of Free Fishermen of the River of Thames", and indeed all ruling bodies of that river since Norman times, also gave the aforementioned line as the limit of their jurisdiction and for the purposes of this paper that limit will be assumed.

The Second Ice Age, it is generally agreed, was responsible for the present peculiar formation of the Estuary. The north-east trend apparently results from the course of the river, when, with the Rhine, it flowed (supposedly) through what is now the North Sea. The supposition is that with the rapid

melting of the ice—the ice barrier ended, as far as Essex was concerned, at what is now the River Crouch valley—a channel was formed to the south, and Britain became an island. This has resulted in an intricate network of currents and a corresponding maze of sandbanks. The peculiar vagaries of the currents persist as far up-river as Gravesend and it is a well-known fact, that, off Southend, while the tide is flowing rapidly to the west, a set of currents may be proceeding in the opposite direction.

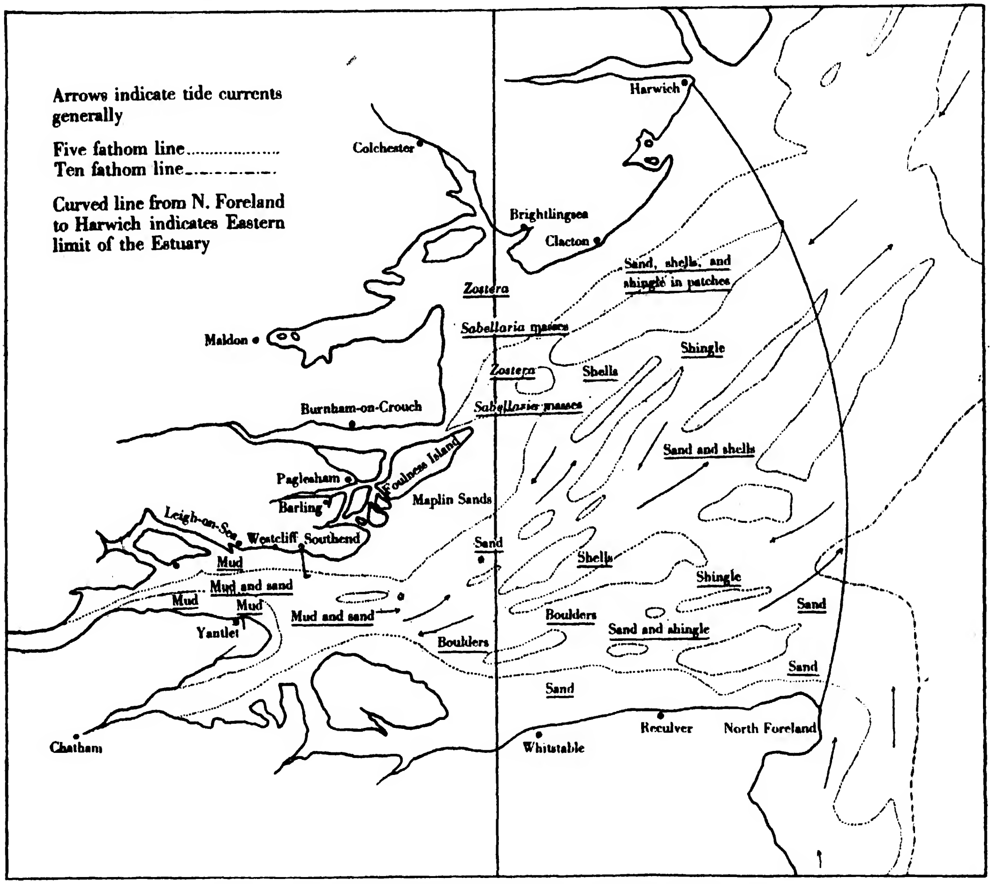


Fig. 1. Thames estuary showing currents and sea bed.

Moreover, there are not infrequently, circular eddies of wind caused by the land mass of the Isle of Thanet and the prevailing north-east winds; these eddies, which have been noted by ballistic experts at the School of Coast Artillery at Shoeburyness, seem to have their origin off Reculver and move in a northerly direction over the Girdler Sands. The unstable currents and the peculiarities of the wind may have some effect on, indeed they may be the reason for, the presence in the plankton of organisms that do not properly belong there.

For these peculiarities alone a survey of the plankton of one particular area may show very different results from one made, say, a hundred yards away. To

complicate matters further the two banks of the river are differently constructed, both physically and geologically.

The Essex bank is low-lying and, in places, characterized by extensive mud flats and large spits of gravel; Foulness archipelago and Canvey Island, the largest of these gravel spits, being reclaimed by the Dutch in the seventeenth century. The Foulness archipelago, consisting of the islands of Potten, Havengore, New England, Wallasea and Foulness itself form a dividing line between

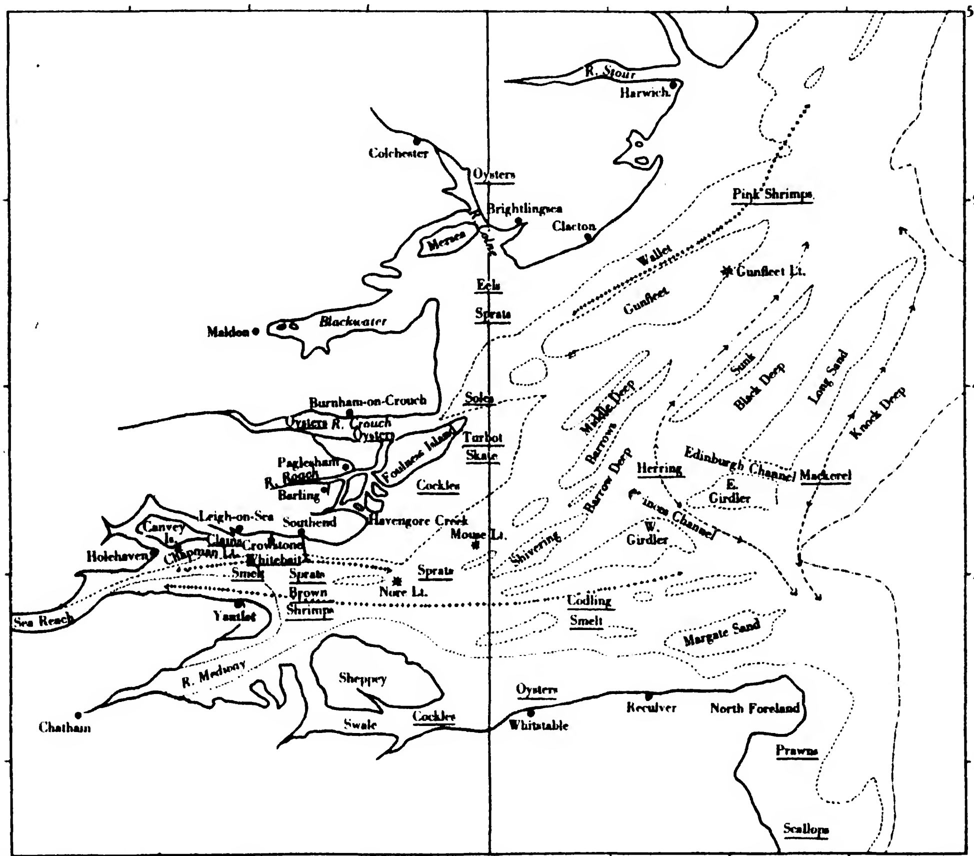


Fig. 2. Thames estuary.

the northern part of the Estuary and the main channels. Foulness Spit, projecting some 15 miles (at low water) to the north-east further emphasizes this division. The southern aspect of Foulness is characterized by the extensive Shoebury, Maplin and Foulness Sands which are contiguous and are noted as cockle beds of great value. The foreshore here slopes gently, the tides receding to the fairway, an average of 2 miles from high-water mark.

The north bank of Foulness is steep-to and in the bight formed by this, the Dengie Flats, and the estuaries of the Colne and the Blackwater, are large stretches of *Zostera*, housing eels and other fishes and a great Crustacean population. The average depth here, at high water, is 5 fathoms. In this

miniature "firth" there is, without doubt, a richer fauna than in any other well-defined part of the estuary. The sheltered aspect is conducive to the breeding of oysters; the *Zostera* makes an excellent spawning ground for fishes with demersal eggs, and the comparatively large tracts of sea-bed covered with the sand-aggregated tubing of *Sabellaria* and *Pectinaria* literally swarm with divers members of the Caridea and other groups of the Crustacea. From the mud of the adjoining creeks the tides bring multitudes of diatoms, mostly Naviculoid.

Conditions on the Kent bank are very different. With the exception of the Medway Estuary and the Isle of Sheppey which divides the mouth of the River Swale, the coast line is more or less unbroken. From Whitstable to the Cant Edge, hard sand is revealed at low water, and the off-shore waters are liberally sprinkled with boulders washed from the London Clay. This same London Clay, from the erosion of Sheppey, is believed to increase the diatom population, and is therefore largely responsible for the food of the Whitstable oysters. The boulders and the rocky aspect of the coast towards the North Foreland attract a more diverse and plentiful number of crabs than elsewhere in the Estuary. Round the Foreland start the scallop beds of the south-east coast. An occasional scallop (the species found hereabouts are *Pecten maximus*, *P. opercularis*, *P. varius* and *P. pusio*) may be dredged west of the Nore, but is considered a rarity. Nevertheless, juvenile scallops and the megalopa stage of crabs, quite unknown to the Essex bank, find their way into the plankton of that side.

The common prawn (*Leander serratus*, Pennant) is most prolific off the North Foreland but its erratic wanderings take it as far up river as Sea Reach. The brown shrimp (*Crangon vulgaris* Linn.) is found everywhere in the Estuary; the pink shrimp (*Pandalus montagui*, Leach), on the other hand, prefers the north-east and more seaward area, increasing in numbers until, off Harwich, it is sufficiently plentiful to warrant a separate fishery. This Pandalid does not breed in the Estuary, an autumnal migration takes them off the Suffolk coast, and there, or possibly somewhere north thereof, they breed. Their larvae have yet to be found in the Estuary proper.

2. Methods

(*a*) *Methods of obtaining samples*

With few exceptions the samples of plankton were taken from the extension at the end of Southend Pier, about 1¼ miles from the shore. Here, at Springs, the water is some 6 fathoms deep. 200 m. nearer midstream there is about 10 fathoms at normal high tides. The principal steamer channels of the Outer Estuary may be as deep as 14 fathoms.

Ordinarily the tide recedes to within a quarter of a mile of the Pier head.

The net principally used was a small Apstein (made of silk containing 60 threads to 1 in.) and this, owing to the strength of the tide, had to be weighted fore and aft with 2 lb. weights. Occasional samples were taken with a 180-mesh Apstein but this net seemed to collect so much silt as to spoil the sample.

Samples taken other than from the Pier head are not here given in detail. They were taken in the River Crouch off Burnham-on-Crouch, Barling Creek, the River Roach at Paglesham, the River Blackwater off Mersea, and off Foulness Point. The Kent coast was not touched, in a plankton sense, during this research; on a number of occasions I have used ordinary beam trawls on that side of the Estuary, principally off the Cant Edge and in Sea Reach, when reviewing the benthic fauna. Regarding the samples taken in the estuaries forming the northern part of the Estuary, these were made usually with the 60 Apstein net; at other times, for purely faunistic purposes, masses of *Zostera* were washed for diatoms and copepods.

The Pier-head samples were taken at roughly fortnightly intervals between 20 November 1933 and 27 November 1934, during which period thirty hauls were made. From November 1934 until April 1937 hauls were made at monthly intervals. For several good reasons the samples were not taken at regular intervals, not the least being that the strength of the tide, at different points of its flood, varies considerably, giving a corresponding variation in the size of the catch (see Fig. 3). As near as possible samples were taken every fortnight. As they were all taken at 12 noon and at 2 hr. before high water, it happened, in practice, that some were a week apart and others as much as 3 weeks.

The net was used from the west side of the Pier and in all cases lowered to 1 m. below the surface for 10 min. Although taken from so near the surface (normally there were 4 fathoms of water at the point used) the haul contained a considerable quantity of sand and other detritus from the bottom. The detritus took the form of spicules from various species of Porifera (sponges), including *Leuconia nivea, Derutus Bucklandii* and *Stelletta* sp. (I have to thank M. Burton, Esq. of the British Museum (Natural History) for the identification of most of the spicules); Echinoderm spines, comminuted pieces of bivalve shells, coal dust, etc. On the other hand, shoals of whitebait at times played around the mouth of the net, yet none occupied any of the samples obtained. The form of the material varied, presumably, according to the strength of the tides; sometimes the greater part of the sample would consist of sand and at others would have the appearance of one taken many miles from shore. The collections are deposited in the Fisheries Laboratory, Lowestoft.

(*b*) *Methods of counting samples*

Immediately on removal from the net the material is killed with formalin. Later it is poured into a large Petri dish and the larger organisms, such as fish larvae, Amphipods, Decapod zooeae, etc., are removed. The remaining material

is then placed in a beaker and the volume made up to 100 c.c. and well stirred. With a graduated pipette 1 c.c. is drawn off and deposited on a squared slide and the organisms contained thereon examined and counted under the microscope.

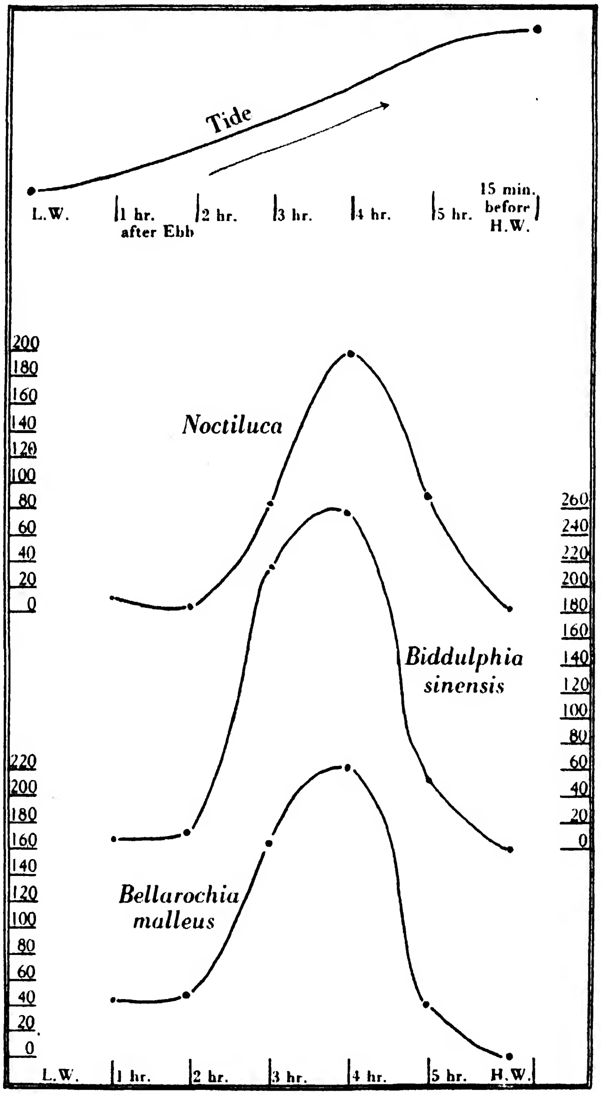


Fig. 3. Variations in the quantities of the three principal organisms of the hauls made at different states of the tide, 17 Sept. 1934, in thousands per ten minutes' haul.

If the sample is a particularly rich one the material drawn off in the pipette is further diluted. The organisms thus counted are multiplied by the extent of the dilution—by 100, 250, 500 or even 1000 as the case might be. By this means the numbers of the predominant organisms can be gauged fairly accurately. The principal drawback to this method of counting is that a small patch of an insignificant organism may form part of the ultimate matter

counted and so give a rather distorted result. This is likely to happen in any form of fractional counting.

The alternative method of placing a small quantity of stirred, but undiluted, material on a slide and counting all organisms up to a hundred—or a thousand, if necessary—and thus arriving at a percentage suffers from the same fault.

Both methods were used in counting the series of samples taken on 17 September 1934. There was no appreciable difference in the actual results.

3. VARIATION IN THE PLANKTON AT DIFFERENT STAGES OF THE TIDE

In order to ascertain more exactly the variation in the plankton at different stages of the tide, on 17 September 1934, I took six samples at hourly intervals —the first at ½ hr. after dead low water and the last at ½ hr. before high water.

Analyses of the six hauls are here given.

½ hr. after ebb. 1.30 *p.m.*

		Macroplankton	
Bellarochia malleus	59,700		
Noctiluca miliaris	8,200		
Biddulphia sinensis	6,300	*Idothea baltica*	13
Chaetoceros subtilis	6,300	Post-larval pipe-fish (*Syngnathus acus*)	2
Lithodesmium undulatum	3,600		
Biddulphia mobiliensis	750	*Gammarus* sp.	1
Actinoptychus splendens	150		
Gasteropod ova	150		
Acartia clausi	150		
Total number of organisms	85,300		

1½ hr. after ebb. 2.30 *p.m.*

Bellarochia malleus	49,500		
Biddulphia sinensis	13,800	Post-larval polychaete	1
Noctiluca miliaris	6,600	*Oikopleura dioica*	1
Chaetoceros subtilis	5,700	*Sagitta elegans*	1
Biddulphia mobiliensis	600	Decapod larvae	1
Lithodesmium undulatum	600		
Polychaete larvae	300		
Acartia clausi	300		
Total	77,400		

2½ hr. after low water. 3.30 *p.m.*

Biddulphia sinensis	217,800		
Bellarochia malleus	163,200	*Idothea baltica*	16
Noctiluca miliaris	84,000	*Sagitta setosa*	2
Lithodesmium undulatum	73,800	*Pleurobrachia pileus*	1
Biddulphia mobiliensis	52,200	*Porcellana* megalopa	1
Chaetoceros subtilis	31,800		
Coscinodiscus concinnus	900		
Acartia clausi	7,200		
Harpacticid sp.	1,200		
Centropages hamatus	900		
Gasteropod ova	900		
Copepod nauplii	600		
Macropsis slabberi	600		
Polychaete larvae	600		
Polychaete post-larvae	300		
Oikopleura dioica	300		
Brachyura larvae	300		
Total	636,600		

3½ hr. after low water. 4.30 p.m.

Biddulphia sinensis	245,400		
Bellarochia malleus	210,000	*Idothea baltica*	53
Noctiluca miliaris	187,200	Pipe-fish, immature (length 12 mm.)	1
Biddulphia mobiliensis	55,800	*Paratylus swammerdami*	1
Lithodesmium undulatum	54,000	*Caprella linearis*	1
Chaetoceros subtilis	12,900	Brachyura larvae	1
Coscinodiscus concinnus	6,600		
Rhizosolenia stolterfothii	1,500		
Nitzschia closterium	300		
Acartia clausi	9,000		
Centropages hamatus	3,000		
Euterpina acutifrons	1,500		
Balanus nauplii	1,500		
Polychaete larvae	900		
Copepod nauplii	900		
Macropsis slabberi	900		
Longipedia scotti	600		
Balanus balanoides, cypris larvae	600		
Oikopleura dioica	600		
Decapod larvae	300		
Gasteropod ova	300		
Harpacticid sp.	300		
Polychaete post-larvae	300		
Total	794,400		

4½ hr. after low water. 5.30 p.m.

Noctiluca miliaris	93,300		
Biddulphia sinensis	55,500	*Porcellana* megalopa	5
Bellarochia malleus	41,100	*Caprella linearis*	1
Chaetoceros subtilis	21,600	*Autolytus prolifer* (metasome larva)	1
Biddulphia mobiliensis	15,000	Larval pipe-fish (length 22 mm.)	1
Lithodesmium undulatum	9,900		
Rhizosolenia stolterfothii	3,000		
Coscinodiscus concinnus	1,800		
Acartia clausi	3,900		
Copepod nauplii	1,200		
Polychaete larvae	600		
Centropages hamatus	600		
Macropsis slabberi	600		
Balanus, cypris larvae	300		
Gasteropod ova	300		
Oikopleura dioica	300		
Pecten sp. juv.	300		
Total	249,300		

½ hr. before high water.

Noctiluca miliaris	4,100		
Biddulphia sinensis	2,300	*Sagitta setosa*	2
Chaetoceros subtilis	1,050	*Caprella septentrionalis*	1
Lithodesmium undulatum	1,000		
Biddulphia mobiliensis	550		
Bellarochia malleus	500		
Rhizosolenia stolterfothii	50		
Copepod nauplii	300		
Centropages hamatus	150		
Total	10,000		

From the foregoing it will be seen that from 2 to 3 hr. before high water, when the tide is "making" at about 2 knots or more, the catch is heaviest (Fig. 3). This, in a measure, is what one would expect, the heavier catches being due largely to the greater efficiency of the net with the swifter tide. The

last haul, made just before the tide was stationary, captured very few organisms; the net floated listlessly in the water at first, and before the 10 min. (as allowed for the previous hauls) had elapsed, it hung vertically, in which position it would have remained for nearly ½ hr., that is, until the ebb carried it eastwards.

There do not appear to be any existing records of the distance covered by the tide in the Thames mouth. The investigations of the Port of London Authority have not been continued beyond Westcliff-on-Sea to the east. As near as one can estimate, however, the tide travels about 5 miles on the flood and about 7 with the ebb. Consequently, the water lying off Southend Pier at high water had been in the vicinity of the Nore Lightvessel 6 hr. previously. Conversely, the water from the Chapman Light, in Sea Reach, ebbs as far as Southend Pier (Fig. 1). The Chapman and the Nore Lights are some 11 miles apart; the average specific gravity of the water at the former is 1020 and at the latter 1022. The Thames at the Chapman Light is barely 4 miles wide, but from that point it widens rapidly until, at the Nore, it is quite 10 miles in width; a further 10 miles eastward finds the Estuary 40 miles across, to all intents and purposes open sea.

Slight as the difference in specific gravity may seem, it is sufficient to control, in great measure, the travels of many estuarine, and some planktonic, organisms. Immature herrings and sprats of the "whitebait", for example, do not journey beyond the Nore to the east and Gravesend to the west; although, two centuries ago, when pollution was less rife, whitebait could be captured as far up river as Blackwall. Before the Port of London Authority took matters in hand there was a possibility that the whitebait would be driven out of the Estuary altogether.

The limits of the plankton Crustacea are governed, largely, by winds, tides and currents. The Harpacticids, however, from their preference for such diatoms as live in the tangled masses of *Zostera*, are more protected, and, although quite a number occur in the plankton proper, for diversity of species and number of individuals, the weed-grown creeks are unequalled.

4. Notes on plankton species

(a) PHYTOPLANKTON

DIATOMS

With the exception of one haul, diatoms dominated the plankton numerically. The haul in question was made on the 3 May 1934, and contained a few scattered groups of *Bacillaria paradoxa* only, and this was the only occasion when Copepods predominated.

Biddulphia sinensis was the most prolific and persistent diatom, and, as it was present in nearly all the samples, it would seem that it is now permanently established in the Thames Estuary. *B. sinensis* is a comparatively recent

introduction to the North Sea, suddenly appearing there in 1903 (**2**), and is usually present in great abundance in the autumn along the eastern side of the Southern Bight. Between 1921 and 1932, it was only found sparingly along the western side (**4**), but following the hot summer of 1933 there was an ex-

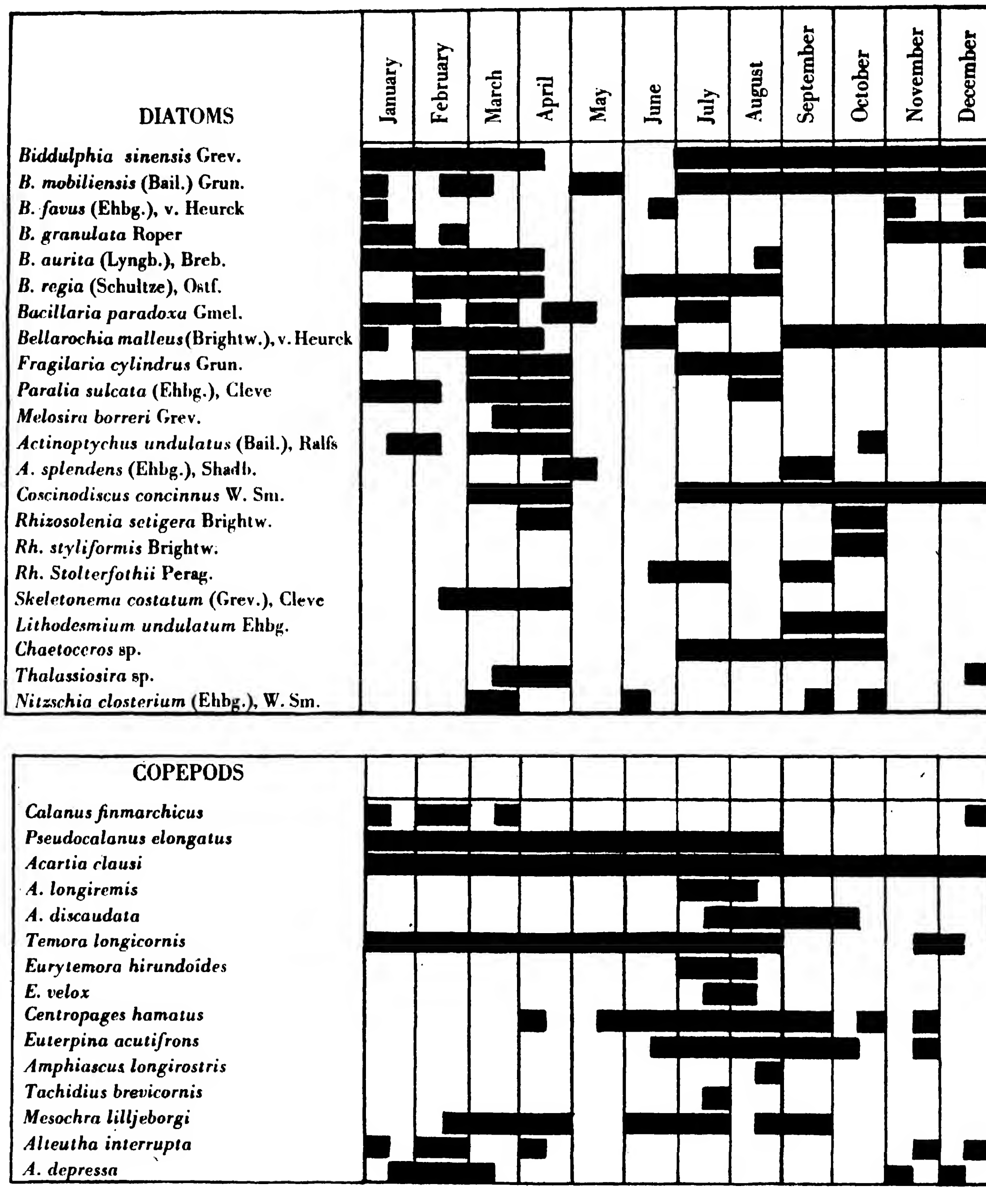


Fig. 4.

ceptionally big development of the diatom, and the concentration spread south-west (**5**). In the following year there were even larger numbers in the south-west. It seems probable that its presence in the Estuary is due to this cause. If this is so, the establishment of a new centre of distribution may have

some effect on the East Anglian autumn herring fishery, as it has been shown (**4**, **5**) that concentrations of diatoms off East Anglia in autumn can seriously affect the shoaling of the herring.

Next to *B. sinensis* in point of consistent profusion is *Bellarochia malleus*. *Skeletonema costatum*, during its brief appearance, was the most abundant, especially in the fine net.

The following tables may convey more clearly the actual diatom variation than if the various species were treated separately. See also Fig. 4.

The most abundant diatoms of each month in order of preponderance

January	February
Biddulphia aurita	*Biddulphia aurita*
Bellarochia malleus	*Bellarochia malleus*
Biddulphia sinensis	*Biddulphia sinensis*
Bacillaria paradoxa	*Bacillaria paradoxa*
Paralia sulcata	*Paralia sulcata*
Biddulphia granulata	*Gyrosigma angulatum*, var. *estuarii*
March	**April**
Biddulphia aurita	*Biddulphia aurita*
B. sinensis	*Bacillaria paradoxa*
Bellarochia malleus	*Skeletonema costatum*
Bacillaria paradoxa	*Fragilaria cylindrus*
Coscinodiscus concinnus	*Biddulphia sinensis*
Biddulphia mobiliensis	*Melosira borrerii*
May	**June**
Bacillaria paradoxa	*Bellarochia malleus*
Biddulphia sinensis	*Rhizosolenia stolterfothii*
Bellarochia malleus	*Biddulphia sinensis*
Fragilaria cylindrus	*B. favus*
	Gyrosigma angulatum, var. *estuarii*
July	**August**
Rhizosolenia stolterfothii	*Biddulphia sinensis*
Chaetoceros densus	*Fragilaria cylindrus*
Biddulphia sinensis	*Chaetoceros densus*
Fragilaria cylindrus	*Biddulphia mobiliensis*
Bacillaria paradoxa	*Paralia sulcata*
Coscinodiscus concinnus	*Coscinodiscus concinnus*
September	**October**
Biddulphia sinensis	*Biddulphia sinensis*
Bellarochia malleus	*Lithodesmium undulatum*
Biddulphia mobiliensis	*Biddulphia mobiliensis*
Lithodesmium undulatum	*Bellarochia malleus*
Chaetoceros subtilis	*Coscinodiscus concinnus*
Coscinodiscus concinnus	*Rhizosolenia styliformis*
November	**December**
Biddulphia sinensis	*Biddulphia sinensis*
Bacillaria paradoxa	*Bellarochia malleus*
Bellarochia malleus	*Bacillaria paradoxa*
Biddulphia mobiliensis	*Biddulphia granulata*
B. granulata	*Actinoptychus undulatus*
B. favus	*Biddulphia mobiliensis*

The following lists give the relative abundance of the various species. The first list relates to such diatoms as are persistently present in fairish numbers, or are exceptionally prolific in their season. The second to what one might call

occasional components, or to those that are consistent members of the plankton, albeit in small numbers. The third list contains the diatoms that were found sparsely, or on only one or two occasions.

Common

Biddulphia sinensis Grev., *B. mobiliensis* (Bail.), Grun., *B. granulata* Roper, *B. aurita* (Lyngb.), Bréb., *Coscinodiscus concinnus* W.Sm., *Bellarochia malleus* (Brightw.), v. Heurck, *Bacillaria paradoxa* Gmel., *Actinoptychus undulatus* (Bail.), Ralfs, *Melosira borreri* Grev., *Paralia sulcata* (Ehbg.), Cleve, *Fragilaria cylindrus* Grun., *Skeletonema costatum* (Grev.), Cleve, *Rhizosolenia stolterfothii* Pérag., *Lithodesmium undulatum* Ehbg., *Chaetoceros densus* Cleve.

Frequent

Biddulphia favus (Ehbg.), v. Heurck, *B. regia* (Schultze), Ostf., *Gyrosigma angulatum* W.Sm., *G. angulatum* var. *estuarii*, *Coscinodiscus marginatus* Ehbg., *C. excentricus* Ehbg., *C. nitidus* Greg., *C. sub-bulliens* Jörg., *Actinoptychus splendens* (Ehbg.), Shadb. *Nitzschia closterium* (Ehbg.), W.Sm., *Licmophora lyngbyei* (Kütz.), Grun. *Chaetoceros subtilis* Cleve, *Rhizosolenia styliformis* Brightw., *R. setigera* Brightw.

Infrequent

Guinardia flaccida (Castr.), Pérag., *Biddulphia rhombus* (Ehbg.), W.Sm., *B. alternans* (Bail.), v. Heurck, *Navicula granii* (Jörg.), *Eupodiscus argus* (Ehbg.), W.Sm., *Ditylium brightwelli* (West), Grun., *Rhizosolenia delicatula* Cleve, *Thalassiothrix frauenfeldii* (Grun.), Cleve & Grun., *Hyalodiscus stelliger* Bailey, *Nitzschia seriata* Cleve, *Thalassiosira hyalina* (Grun.), *T. nordenskioldii* Cleve.

The diatoms from the mud and *Zostera* masses of the adjacent creeks vary in great measure from those given above. To generalize, the creek diatoms are almost entirely Naviculoid, so also are those from the surface mud of the foreshore at Westcliff-on-Sea, the exception in the latter case being *Biddulphia favus* which is fairly common at times. The light surface sand of the cockle beds off Foulness Island contains similar diatoms plus some of the smaller *Coscinodiscus* species; it is this type of diatom that is found more commonly in the gut of the cockle (*Cardium edule* L.), and not those of the plankton of the same district.

(b) ZOOPLANKTON

RHIZOPODA

Polythalamia

Foraminifera were present in all samples in greater or lesser degree. With strong, scouring tides, 10% or more of the bulk of the samples would consist of Foraminifera. On the mud of the foreshore I found a fair number, mostly *Nonionina* sp.; on the beach at Foulness Point, and, in particular, along the edges of a tidal dyke behind the seawall, I found most of the types that occupied the plankton samples. These are enumerated below in the order of their preponderance.

Polystomella striato-punctata (F. & M.), *Miliolina* sp., *Biloculina* sp., *Nonionina* sp., *Planorbulina mediterranensis* d'Orb., *Lagena striata* (d'Orb.), *Textularia variabilis*.

Cystoflagellata.

Noctiluca miliaris Surir.

Although sporadic in appearance *Noctiluca* were present in at least one sample during the month throughout the year, usually in fairly great numbers. They did not appear only when the weather had been warm; for example, on 3 December 1933 during a bitterly cold easterly gale which had been blowing for some days, the catch included *Noctiluca* in proportionately large numbers. In August and September they were most abundant and in those months nearly all specimens observed contained the diatoms *Rhizosolenia stolterfothii* and *Paralia sulcata*. They were most prolific in the sample taken on 17 September 1934, when 84,000 were present.

DINOFLAGELLATA

During the winter of 1933–4, when the 180-mesh Apstein net was in use, the following Dinoflagellates, averaging 500 of each species per haul, were identified.

Ceratium furca Ehbg.
C. fusus Ehbg.
C. tripos Nitzsch.
Ceratium macroceros Ehbg.
Peridinium depressum Bail.

CILIATA

Tintinnoidea

Tintinnopsis campanula (Ehr.) Dad.

Very few Tintinnids were found in the 60-mesh net, but during the time that the 180-mesh net was used large numbers were captured. Of the various species taken at one time or another the above was the only one that I could identify.

FLAGELLATA

Phaeocystis sp.

Phaeocystis usually appeared in the plankton in mid-May, as a faint trace, and increased until mid-August. By September, however, the water is quite clear. The whitebait, when *Phaeocystis* is in evidence, seek the creeks and the inshore water; in fact, during those months when it is at its height the whitebait fishermen pursue their calling from the beach itself by means of dragnets. This they have done for many years. The fishermen say that "'bacca juice" is always more prevalent after a mild March and April and also that if it is found early in the year then it will be very abundant and will remain longer in the Estuary.

COELENTERATA

Anthomedusae

Bougainvillea britannica Forbes.

One specimen only, 7 March 1934.

Sarsia tubulosa (Sars).

Two specimens, April 1934.

Podocoryne carnea Sars.

Scattered specimens (half a dozen in each haul) from March to May.

Rathkea octopunctata (M. Sars).

This species literally swarms in the Estuary from March to April at which times it occupies at least half of the bulk of the catch.

Leptomedusae

Obelia nigra E. T. Browne.

In fair numbers between January and March only.

Phialidium hemisphericum (Peron & Lesueur).

This is the most abundant of the Medusae between June and October. The largest catch was on 31 July 1934 when 240 were present.

Discomedusae

Aurelia aurita L., and *Cyanea capillata* L.

Young specimens, 4–10 mm. in length, were taken during early summer.

CTENOPHORA

Pleurobrachia pileus Flem.

Sporadically, and never more than six in one haul, between February and September.

ECHINODERMATA

Asteridae

Bipinnaria of *Asterias rubens* L.

A few were found in the summer hauls.

Echinopluteus of *Echinus miliaris* Leske.

This is the only member of the Echinidae found on the adjacent and extensive Maplin Sands. The pluteus is not common in the catch, although the spines, together with *Alcyonium* and sponge spicules, are a feature of hauls taken on strong tides.

CHAETOGNATHA

Sagitta setosa (J. Müller).

Present at all seasons.

Sagitta elegans (Verrill). Also a constant member of the plankton but in fewer numbers than *S. setosa.*

The occurrence of *Sagitta elegans* so close to the shore in the southern North Sea is at variance with the picture of the distribution of this species we should have expected from the work of F. S. Russell (**3**). As *S. elegans* is considered as an indicator of Atlantic water, the following records of its occurrence in the Thames Estuary might be of some interest:

1933. 20 November, 3 and 21 December.

1934. 5 and 25 January, 3 and 21 February, 7 and 27 March, 17 April, 17 September.

POLYCHAETA

Autolytus prolifer O. F. Müll.

Occasional specimens taken during the winter months.

Magelona sp.

Nectosome and post-larvae in September only.

Terebella sp.

Post-larval forms present at intervals throughout the year.

The various larval forms of Polychaetae are present in constant numbers throughout the year.

CRUSTACEA

CIRRIPEDIA

Balanus balanoides L.

Both the cypris and the nauplius larvae, as well as exuviations of the adult, were present in every sample throughout the year. Nevertheless, one week would find them abundant, another would find them sparse; but in no case could a reason be adduced for the variation.

COPEPODA

Calanoidea

Calanus finmarchicus (Gunner).

On one occasion only were adults of this Copepod found (21 December 1933), 240 being present. Immature specimens, on the other hand, were a feature of the hauls during spring.

Pseudocalanus elongatus Boeck.

Except during the summer this species was fairly common, being present in numbers varying from 100 (1 June 1934) to 2000 (5 January 1934).

Centropages hamatus (Lilljeborg).

In late spring a sprinkling of immature specimens were found, by mid-summer the adults were present and remained in the plankton until October. In no instance did they dominate the Copepod content.

Temora longicornis (O. F. Müll.).

A steady population of this Copepod marked nearly all samples. Spring and autumn were the most prolific months when as many as 3000 specimens were found in one sample (17 April 1934).

Eurytemora hirundoides (Nordquist).

Found only during August and September, and then in but few numbers, in 1934. This applied also to the years 1935 and 1936. In 1937, however, a haul made in the first week of April captured 5500 specimens.

Eurytemora velox (Lilljeborg).

Although I did not find specimens of this species in the plankton samples taken from Southend Pier I have taken it, in September, in the Crouch Estuary off Burnham.

Acartia clausi Giesbrecht.

This is by far the most common Copepod in the Thames Estuary plankton, outnumbering, save in very few instances, the sum total of all the other species. It was present in every sample without exception.

Acartia longiremis (Lilljeborg).

Apparently this is solely a summer visitor; it was observed only during August and September when it was in the proportion of one to five of *A. clausi*.

Acartia discaudata (Giesbrecht).

Present in August and September only, but in greater numbers than the foregoing.

Harpacticidae

Longipedia coronata Claus.

A few specimens were obtained in September 1934.

Euterpina acutifrons (Dana).

Fairly common from February to October.

Amphiascus longirostris (Claus).

In quite large numbers in the sample of 27 August 1934 but not noticed in any others.

Tachidius brevicornis Lilljeborg.

On 31 July 1934 the haul contained 150 specimens.

Mesochra lilljeborgi Boeck.

Likewise a summer visitor.

Alteutha interrupta (Goodsir).

I have taken this, and the following Harpacticid, from the surface mud off Westcliff-on-Sea; on occasion during the winter and spring, specimens of both have been in the catch.

Alteutha depressa Baird.

If anything this species is more numerous than the last.

Cladocera

Podon intermedius Lilljeborg.

One specimen only was found and that on 27 August 1934.

Amphipoda

Gammarus locusta (L.).

Found in sparse numbers during spring.

Gammarus marinus Leach.

Found occasionally in spring and summer.

Gammarus duebeni Lilljeborg.

This was the most common of the Gammaroidea; even so, no sample contained more than five specimens. They were present at all seasons.

Paratylus swammerdami (Milne-Edwards).

One specimen, 17 September 1934.

Caprella linearis Spence Bate.

Very common from May to October.

Caprella septentrionalis Kröyer.

A few specimens were found in the hauls during October.

Phtisica acaudata (Gron.).

This Amphipod was represented in nearly every sample throughout the year. The greatest numbers were taken in September.

The following Amphipods, although not noticed in the samples taken from the end of Southend Pier, were present in hauls made in the Northern part of the Estuary:

Apherusa bispinosa (Spence Bate).
Dexamine spinosa (Mont.).
Aora typica Kroyer.
Corophium bonelli Milne-Edwards.
Unciola crenatipalmata Spence Bate.

Isopoda

Idothea baltica (Pallas).

Sporadic, although fairly common in the catch during the summer months. Sixty specimens were present in the catch of 3 September 1934. Ordinarily they are frequently found in the nets of the local shrimpers and whitebaiters.

Cumacea

Pseudocuma longicorne (Spence Bate).

An occasional specimen was to be found in the spring and summer hauls.

Pseudocuma similis G. O. Sars.

This species was fairly common during winter and spring.

Mysidacea

Gastrosaccus normani G. O. Sars.

A few specimens were found in several of the winter hauls.

Gastrosaccus sanctus (van Beneden).

Represented in the sample of 3 February 1934.

Gastrosaccus spinifer (Goës.).

One specimen only was found and that was on 3 May 1934.

Siriella clausi G. O. Sars.

Three individuals were in the sample of 31 July 1934.

Schistomysis ornata G. O. Sars and *S. spiritus* Norman.

These Mysids were in most of the samples taken during February, March, and April, but never exceeding ten specimens in any one sample.

Macropsis slabberi van Beneden.

This was by far the most common Mysid and was present in nearly every sample throughout the year; in the summer months as many as three or four hundred would be found in the net. The average length was 11 mm. and never exceeded 14 mm.

DECAPODA (MACRURA)

Crangon vulgaris L.

I had anticipated making consistently large hauls of the larvae of this shrimp throughout the year. In the summer the adults congregate in the warmer water of the swins and runnels close inshore, consequently one would not expect to find many individuals near the surface at a mile from the beach. On the other hand, as there are undoubtedly three (possibly more) breeding periods of *Crangon vulgaris* during the year, there should be many immature specimens in the deeper water such as obtains off Southend Pier. The older females bury themselves in the sand or mud of the sea-bed during cold weather but the males and the young remain between the bottom and mid-water. Moreover, as the tide retreats to within two or three hundred yards of the pier head, even in summer it would be natural to expect, at the least, a sprinkling of immature specimens at all seasons. The sum total of immature members of this particular species captured was one only and that on 7 February 1934, the length being 18 mm.

There is a possibility that a net with a coarser mesh would have met with a greater measure of success. Nevertheless, on occasion, an adult male, 25–35 mm. in length was captured and, as will be seen, a number of larval fishes, besides adults of *Leander squilla*. This seems to indicate that the fine mesh was not alone responsible for the paucity of specimens. Neither have I taken larval shrimps in the more seaward areas of the Estuary, i.e. the Blackwater—Crouch estuaries. From the foregoing I am inclined to think that *Crangon vulgaris* breeds and develops in the more brackish water, such as obtains between Holehaven and Gravesend; or, in any case, more so than off Leigh and Southend where the shrimp fishery has its headquarters.

Leander squilla L.

An occasional specimen of this prawn, locally known as the "white shrimp", was found during November and December but at no other time.

Palaemonetes varians (Leach).

No specimens were found in the samples taken off Southend Pier. Samples from the Crouch mouth contained adults and a very few larvae. In spring, however, the salting pools literally swarm with larvae of from 6 to 10 mm. in length. Strangely enough, although the adults will survive the transition from brackish water to a freshwater aquarium and will live for many months under such conditions, the larvae die in the course of a few hours.

DECAPODA (ANOMURA)

Porcellana longicornis L.

From the middle of August to the end of September the net contained from 10 to 50 megalopa larvae of this crab in the various hauls. Ordinarily the adult does not inhabit the north bank of the Estuary: the Kent side is more favoured, and the presence of these megalopae seems to suggest a mingling of currents in the vicinity of, say, the Mouse Lightvessel. Other organisms, such as larval molluscs, which do not come in the Essex fauna as adults, were found at times in the plankton in various stages of development.

DECAPODA (BRACHYURA)

Carcinus maenas Penn.

The zoea larvae of the common shore crab appear towards the end of March and occupy the plankton until July; by the end of August the megalopa take their place.

MOLLUSCA

LAMELLIBRANCHIATA

Pecten sp. juv.

From May until mid-summer specimens were present in the net, their numbers being greatest in May. Of the various species of *Pecten* inhabiting the Thames Estuary none is found in any abundance either to the north or west of the Nore Sand. An occasional individual may wander from its usual ground but, generally speaking, the principal scallop area does not start until the North Foreland has been rounded.

Cardium edule L.

From April until August larval cockles were present in great numbers, the peak period being mid-June. I have not seen the veliger stage at all.

Lamellibranch sp. var.

The larval stage of various other lamellibranchs are featured in early summer. *Mya*, *Tellina*, etc. are the principal genera represented.

GASTROPODA

Littorina littorea L. Ova.

From March until the end of August the ova of the common periwinkle were present in the haul, the two peaks being in the first week of March and the last week of June. With the exception of one haul which contained 60 specimens (27 November 1933) none were in the catches made between the end of August and the beginning of March. W. M. Tattersall (6) refers to the protracted breeding season of this Gastropod and there can be little doubt that, in the Thames Estuary in any case, the breeding season extends over at least six consecutive months. The veliger stage was noticed in the plankton during July and August principally, although in succeeding months a few were present.

TUNICATA

Oikopleura dioica Fol.

This Appendicularian was first noticed in the samples taken in May when 60 were found in one haul. The numbers gradually increased until on 9 October the net contained 1000. On 29 October 1934 their numbers fell off and after that date they were entirely absent.

FISHES

Syngnathus rostelatus Nilss.

This, the only adult fish found in the plankton, was first recorded from the Thames Estuary from specimens found in the sample of 20 November 1933. I am indebted to Dr J. R. Norman, British Museum (Natural History), for identifying the specimens.

Syngnathus acus L.

Immature specimens, closely resembling the adult *S. rostelatus*, were present during July and August.

Clupea sprattus L.

Between June and August 1934, a very few specimens (never more than three in any one haul) were present in the net. These varied in length from 6 to 9 mm.

Clupea pilchardus Walbaum.

Six specimens on 22 June 1934.

Clupea harengus L.

In March a fair number of immature herrings were in the plankton, the length being from 13 to 16 mm. Specimens taken in late April were very few and measured 15–17 mm. One specimen was taken 27 August 1934 and this was 21 mm.

Pleuronectes sp.

In March and April in most years small, immature flat fishes were in the catch. The length varied between 7 and 10 mm.

Leptocephalus morrisii Gmelin.

In March 1933 whilst trawling for shrimps off the Chapman light the trawl contained, among other things two specimens of *L. morrisii*, length 75 mm. They were alive when captured.

Fish ova, pelagic.

On 1 June 1934, the only fish egg was obtained, probably of the flounder, but I cannot be certain of this. Contrary to my expectations, eggs were disappointingly few. Numerous fishes with pelagic eggs breed within the precincts of the Estuary; that only one was found was surprising. However, at some future date, I hope to take samples from other parts of the Estuary with a view to obtaining some data on the breeding habits of such fishes as the sole, plaice, dab, herring, sprat, whiting and pilchard.

5. General inferences

The foregoing list of planktonic organisms shows a typical littoral flora and fauna. With a few exceptions the Inner Estuary, at least, seems to have nothing surprising to reveal. The exceptions, however, give one the impression that the Outer Estuary in the vicinity of, say, the Edinburgh and the Princes Channels to the south-east and the Wallet, the Middle, Black and Barrow Deeps to the north-east and, in particular, the Kentish Knock Light to the East, might exhibit less estuarine features. To the best of my knowledge these areas have yet to be examined thoroughly. Indeed, with the exception of Dr James Murie's report on the Thames Estuary Sea Fisheries (**1**), the Thames Estuary has been surprisingly neglected by zoologists. Of the four main fisheries of the district, viz. cockling, shrimping, spratting and whitebaiting, only spratting is not dependent on the plankton of the Estuary for its maintenance. It is true that if the decline in those fisheries locally is maintained, they will cease to exist within the next twenty years or so. At one time they were worth many thousands of pounds annually to the Leigh and Southend fishermen. There are several reasons for the decline, also there are not a few reasons why there should not be a decline—one cannot always lay the blame at the door of pollution.

The prescience of the fishermen regarding the whereabouts of his prospective catch at different seasons is truly astounding; nevertheless, the Outer Estuary is in great measure *terra incognita* to most of the present-day Leigh

fishermen. Yet there are fish to be caught in the more distant and deeper swins; the crew of one of the spratters for the past two seasons, after the spratting time was over, set out long lines in the Middle Swin with surprising results. The area in question, if it were better understood, could produce a fishery of miscellanea (sole, turbot, brill, etc.) that would pay better than the present fisheries do.

In all, including the sharks and rays, over 100 different species of fish have been captured at one time or another within the confines of the Estuary. Of this number, apart from whitebait and occasional Peter netting for plaice, sprats alone are fished for; these constitute, perhaps, one of the least profitable of fisheries.

The Inner Estuary is undoubtedly rich in food for small fry and this must have its repercussion as regards the food of larger organisms in the more seaward areas. For this reason alone, i.e. that of fostering an additional fishery, I feel that further research is necessary.

6. Acknowledgement

I would like to take this opportunity of conveying my thanks to the Director and to the plankton staff of the Fisheries Laboratory, Lowestoft, for the facilities they gave me for studying plankton at the Laboratory, and to the latter for their assistance in compiling this paper.

7. Summary

The results of a phyto- and zooplankton survey in the Thames Estuary from November 1933 to April 1937 are described. Most of the survey was done at Southend-on-Sea. In lesser degree the waters in the vicinity of Mersea and Burnham-on-Crouch were studied. The seasonal changes are analysed, with special reference to diatoms and Copepods, also the relation of plankton to the tides. The plankton of the Thames Estuary forms the principal food of the cockle, whitebait and the shrimp, all of which are fished extensively and are capable of greater development. There are large oyster beds, principally at Colchester and Whitstable; the oyster depends almost entirely on diatoms for its food.

REFERENCES

1. **Murie, J.** (1903). "Report on the sea fisheries and fishing industries of the Thames Estuary." London.
2. **Ostenfeld, C. H.** (1908). "On the immigration of *Biddulphia sinensis* Grev. and its occurrence in the North Sea during 1903–7." Medd. fra Kommissionen for Havundersøgelser, Ser. Plankton, 1, No. 6. Copenhagen.
3. **Russell, F. S.** (1935). "On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea." J. Mar. Biol. Ass. U.K. 20: 309–32.
4. **Savage, R. E. & Hardy, A. C.** (1935). "Phytoplankton and the herring. Part 1." Minist. Agric. Fish., Fish. Invest. Ser 2, 14, No. 2.
5. **Savage, R. E. & Wimpenny, R. S.** (1936). "Phytoplankton and the herring. Part 2." Minist. Agric. Fish., Fish. Invest. Ser. 2, 15, No. 1.
6. **Tattersall, W. M.** (1920). "Notes on the breeding habits and life history of the periwinkle." Fish. Ireland, Sci. Invest. 1920 Dublin.

TEMPERATURE AND THE INCIDENCE OF CERTAIN SPECIES IN WESTERN EUROPEAN WATERS IN 1932–1934

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1. Introduction

In the course of an investigation into the relation between the quantity of brood in certain Lamellibranch Molluscs and weather conditions (Stephen, 1938), a well-marked rise in the value of the mean air temperature in certain areas for the years 1932–4 was noticed. These years were remarkable for the incursion into British waters of species which do not usually occur so far north, and also for the specially large broods recorded for several species.

So far little notice seems to have been taken of this period as a whole, although numerous isolated records of the unusual spread of various animals have been given. The object of these notes is to draw attention to the general course of events, and it is hoped that others may add to the records. Since the species affected were in several cases of economic value it is important that as complete a record of the period as possible should be made.

My thanks are due to Major A. H. R. Goldie of the Meteorological Office, Air Ministry, for supplying me with the figures for temperature.

2. Northward spread of organisms

The first evidence that animals usually found in more southern waters were entering British seas was contained in a letter to *Nature* (Kemp & Russell, 1932), where the appearance of *Velella*, *Ianthina* and *Salpa fusiformis* at Plymouth was recorded. Soon after (Stephen, 1932) it was reported that conditions were also abnormal in Scottish waters and, more especially, that whales and dolphins were more than usually common. Later it was reported (Farran, 1933) that the pelagic Tunicate, *Cyclosalpa bakeri*, a tropical form, had been taken 50 miles south-west of the Fastnet Light in August 1932; also that blue sharks (*Carcharinus glaucus*) were more than usually abundant. *Physalia*, *Velella* and *Ianthina* were also recorded as being abnormal in their distribution in New Zealand waters (Dakin, 1933).

Still more widely noted and of much more economic interest in certain countries, was the appearance of a disease of the eel-grass (*Zostera*) over wide areas. This disease seems to have spread very rapidly along the Atlantic coast of North America. It was first observed at the end of 1931 on the coast of Virginia. From there it spread north to Nova Scotia. In 1932 it was next met with on the coasts of Europe and spread to Denmark in 1932–3 (Petersen, 1935).

Coming more particularly to Scottish waters, a survey of the records shows that a similar invasion was taking place and that a number of species was concerned. Some appeared as late as 1935 so that the "invasion" was spread over a long period.

In the first place the number of whales and dolphins stranded on the Scottish coast (excluding the false killer, which is very erratic in its time of appearance and sometimes strands in shoals) while varying from year to year, is usually fairly low. In 1932, however, there was a sharp rise in the numbers stranded, showing that these animals were either more abundant or that the waters close to the Scottish coast were more favourable for them. The following were the numbers stranded:

1929	1930	1931	1932	1933	1934	1935
3	2	9	20	8	5	4

Three interesting species of fishes were noticed in Scottish waters during the same period. The long-finned tunny (*Thynnus germo*) whose only previous Scottish record was from Orkney in 1900, was taken twice during the period. The first record was from Lochgoilhead, Firth of Clyde, in 1933 (Stephen, 1933*a*), the second record from the Holy Loch, Firth of Clyde, in June 1934 (Stephen, 1934). In 1933 the saury pike (*Scombresox saurus*) invaded the Firth of Forth (Stephen, 1933*b*). This fish was also recorded from the Yorkshire coast in December 1932 and January 1933 (Clarke, 1933), and from the Isle of Man (Rept. Mar. Biol. Sta. Port Erin, 1933, p. 34). In April 1931 two specimens of the small shark, *Oxynotus paradoxus*, were taken 70 miles north-north-west of the Fastnet Light on the south-west coast of Ireland, this being the first record for British waters (Norman, 1932). The first and only recorded Scottish specimen was taken a year later in the Minch in March 1933 (Stephen, 1933*c*).

The pelagic Tunicate, *Cyclosalpa bakeri*, already reported as being taken on the south-west of Ireland (Farran, 1933), appeared in the Fair Isle passages and on the north of Scotland in November 1932 (Ann. Rep. Fish. Bd. Scotland, 1932, p. 68), this being the first Scottish record. The cuttlefish, *Sepia officinalis*, also invaded the North Sea in large numbers. In the Ann. Rep. Fish. Bd. Scotland, 1934, p. 54, it is reported as being present in the years 1932 and 1934. In 1934 it was very common, as may be judged from the report kindly given me by Mr J. Macpherson. He informed me that on one trip he was fishing in the area 90 miles east by north to 140 miles north-east by east from Aberdeen in depths from 60 to 80 fathoms and that he had taken about 200 on the trip. Up to ten were being taken in a 3 hr. haul with the trawl. He considered, however, that they had only been common for the last year or two. Specimens were also reported from Iona and from the Clyde, this latter being the first record of the species in the Millport area. Living *S. officinalis*, were also recorded for the first time from the Isle of Man, specimens being taken in September 1934. (Rep. Mar. Biol. Sta. Port Erin, 1934, p. 26). Another

cephalopod, *S. elegans*, was recorded for the first time from Scotland at Barra, in July 1935 (Forrest and others, 1936).

The pelagic Mollusc, *Ianthina britannica*, already mentioned as having been reported from Plymouth in 1932, appeared in large numbers on the west coast of Scotland in the summer of 1935 in Skye and in the Outer Hebrides (Beatson *et al.* 1936). In most cases it was accompanied by the Siphonophore, *Velella*, and the floating barnacle *Lepas fascicularis*. *Velella spirans* and *Noctiluca scintillans* occurred off the Isle of Man, having appeared in large numbers in October and July 1934, respectively. (Rep. Mar. Biol. Sta. Port Erin, 1934, p. 26).

An interesting series of records was given by Elmhirst (1936) showing the recent changes of the status of several species in the Clyde. Some species showed marked fluctuations during, or after, 1932. Since 1933 the summer invasions of the basking shark (*Selache maxima*) have been noticeable. Since 1932 also, there seems to be some evidence of the re-establishment of the once abundant bivalve, *Spisula subtruncata*. Young *Aplysia punctata* were present in large numbers in 1934. *Echinocardium cordatum*, scarce for a few years subsequent to 1920, became abundant again. Certain other species have become scarce in the area.

3. Production of brood

The amount of brood produced by certain species is also worthy of notice. In the southern North Sea an abundant herring brood appeared in 1932 (Hodgson, 1934, p. 63). This was a year before it was predicted and was a break in what appeared to be a definite 3-year cycle for this species. As against this successful herring brood, that of the haddock in Scottish waters was very poor for the 3 years 1932–4, that is during the period of high temperatures (Ann. Rep. Fish. Bd. Scotland, 1936, p. 61). In the Limfjord in Denmark, the oyster, which had not been known to spat since 1919 and was in danger of dying out, produced considerable spat in 1932 and 1934. Spärck (1935) attributes this to the high temperatures then prevailing.

In the Clyde area both *Tellina tenuis* and *T. fabula*, in which the incidence of broods has been closely studied since 1926, produced, in the autumn of 1932, broods several times in excess of any previously noted. Other species were observed to be breeding freely but were not studied quantitatively. There seems also to have been a large settlement of brood of *Mactra stultorum* off Montrose in 1933, to judge by the quantities of shells, measured and age estimated, which were washed up in the summers of 1934 and 1935.

4. Temperature correlations

As was to be expected from the increased air temperatures, the temperature of the surface waters in the North Sea was above normal. In the northern North Sea it was some 1·5–2° C. above normal in 1932. Salinities were also

high (Ann. Rep. Fish. Bd. Scotland 1932, p. 67; also Tait, 1935). In 1933 the temperatures were 2–3° C. higher. In the southern North Sea the same thing was found. In 1933 in the early part of the herring fishing season the temperature was about 2° C. above normal for that time of year (Hodgson, 1934, p. 103). These high temperatures seem to have been responsible for the growth of dense patches of diatoms which adversely affected the herring fishing by forming a barrier which was avoided by the migrating herring (Savage & Wimpenny, 1936).

The incursions of species already mentioned seem possibly to have been as much due to the favourable habitat caused by a general warming up of the northern Atlantic surface waters as by a greater northward flow of Atlantic water of southern origin, as already suggested by Farran, if one may judge from the higher air temperatures recorded from both sides of the Atlantic at the same time. These have been analysed for four stations, namely Florida, Rothesay, Lowestoft and Gaardbogaard, Denmark. The means for the whole year, and for the summer are shown in Table 1. Taking the temperature

Table 1

Temperatures in ° F.

(*a*) Yearly means

	1930	1931	1932	1933	1934	1935
Florida	74·6	74·2	75·9	76·0	75·3	74·9
Rothesay	47·3	47·1	48·0	48·7	48·8	47·8
Lowestoft	49·4	48·1	49·2	51·0	50·2	50·0
Gaardbogaard	46·5	43·8	45·7	45·9	47·2	45·4

(*b*) Means for April to September

	1930	1931	1932	1933	1934	1935
Florida	80·3	79·5	80·0	80·6	80·1	80·6
Rothesay	53·1	51·9	52·6	54·9	53·5	53·4
Lowestoft	55·9	54·5	55·8	57·9	56·6	56·6
Gaardbogaard	54·9	52·1	54·2	55·5	55·2	53·7

(*c*) Difference between successive yearly means

	1930–1	1931–2	1932–3	1933–4	1934–5
Florida	−0·4	+1·7	+0·1	−0·7	−0·4
Rothesay	−0·2	+0·9	+0·7	+0·1	−1·0
Lowestoft	−1·3	+1·1	+1·8	−0·8	−0·2
Gaardbogaard	−2·7	+1·9	+0·2	+1·3	−1·8

(*d*) Differences between successive summers

	1930–1	1931–2	1932–3	1933–4	1934–5
Florida	−0·8	+0·5	+0·6	−0·5	+0·5
Rothesay	−1·2	+0·7	+2·3	−1·4	−0·1
Lowestoft	−1·4	+1·3	+2·1	−1·3	0·0
Gaardbogaard	−2·8	+2·1	+1·3	−0·3	−1·5

gradients for the whole year (Table 1 (*c*)) it is seen that at all stations 1931 was colder than 1930, but in 1932 there was a rapid rise. 1933 was a little warmer than 1932, but by 1934 the temperature was falling at Florida and Lowestoft, and in 1935 there was a fall at all stations.

The same general course was followed by the summer temperatures (Table 1 (*d*)). 1931 was much colder than 1930, but the 1932 figures showed a considerable rise at all stations. This rise was even more marked in 1933.

There was a fall at all stations for 1934. The figures for 1935 showed little difference from those of the previous year.

That this "warming up" was a phenomenon of widespread incidence is further evidenced by the fact that the winter of 1933–4 in the Pacific north-west was unusually mild, the mean air temperature being 7·2° F. above the winter normal (Keyser, 1934).

One further point of interest arises. Mention has already been made of the incursion of *Velella* and other forms into New Zealand waters, recorded by Dakin, in 1933. The air temperatures for Dunedin N.Z. have been examined and it is of interest to see that they form a parallel with the conditions in other waters just described, only the rise started a year later and continued longer than in the north. The mean air temperatures were as follows:

1931	1932	1933	1934
50·5 F.	50·4 F.	51·3 F.	51·9 F.

5. SUMMARY

Abnormally high temperatures in the Atlantic in the years 1932–4 were accompanied by unusual frequency and abnormal migration of certain marine animals, as deduced from records made round the coasts of the British Isles.

REFERENCES

Beatson, J. B., Nicol, E. A. T. & Elton, C. (1936). Scot. Nat.: 27.
Clarke, W. J. (1933). Naturalist: 100.
Dakin, W. J. (1933). Nature, Lond., 131: 239.
Elmhirst, R. (1936). Ann. Rep. Scot. Mar. Biol. Ass. 1935–6: 11.
Farran, G. P. (1933). Nature, Lond., 131: 240.
Forrest, J. E., Waterston, A. R. & Watson, E. V. (1936). Proc. R. Phys. Soc. Edin. 22: 290.
Hodgson, W. C. (1934). "The natural history of the herring of the southern North Sea." London.
Keyser, E. M. (1934). Bull. Amer. Meteor. Soc. 15: 257.
Norman, J. R. (1932). Proc. Zool. Soc. Lond.: 77.
Petersen, H. E. (1935). Rep. Danish Biol. Sta. 40: 3.
Russell, F. S. & Kemp, S. (1932). Nature, Lond., 130: 664.
Savage, R. E. & Wimpenny, R. S. (1936). Min. Agric. and Fish., Fish. Invest. Ser. 2, 15, No. 1.
Spärck, R. (1935). Rep. Danish Biol. Sta. 40: 39.
Stephen, A. C. (1932). Nature, Lond., 130: 889.
Stephen, A. C. (1933a). Scot. Nat.: 26.
Stephen, A. C. (1933b). Scot. Nat.: 95.
Stephen, A. C. (1933c). Scot. Nat.: 85.
Stephen, A. C. (1934). Scot. Nat.: 128.
Stephen, A. C. (1938). J. Anim. Ecol. 7: 130.
Tait, J. B. (1935). Rapp. Cons. Explor. Mer. 94 (3): 60.

PRODUCTION OF LARGE BROODS IN CERTAIN MARINE LAMELLIBRANCHS WITH A POSSIBLE RELATION TO WEATHER CONDITIONS

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(*With 6 Figures in the Text*)

CONTENTS

1. Introduction

In many species of animals it is only in certain years that there is a very large production of young, or at least of young which survive to form later, as a dominant year-group, a large proportion of the population. The problem of the underlying causes of these productive years is one of considerable economic importance. For example, it is now well known in fishes such as the haddock and the herring that successful broods are produced only at irregular intervals, and that such broods form the basis of the fishery for some years afterwards. So, too, with the small intertidal Lamellibranch Mollusc, *Tellina tenuis*, it is only in certain years that a successful spatfall occurs. Sampling of the population of this species in Kames Bay, Millport, begun in 1926, has been continued regularly. In that period there have only been four successful spatfalls, in the years 1926, 1930, 1933 and 1936 (Fig. 1).

It was thought possible that alterations in the physical conditions of the environment might be the chief causes of these variations in the quantity of brood. Since the annual shift of the modes has been about the same, even in the years with very large broods, it may be assumed that the food supply has always been sufficient. The species being an intertidal one, the chief variable physical factors affecting the environment are temperature, sunshine and rainfall. This paper deals principally with the fluctuations of these factors from

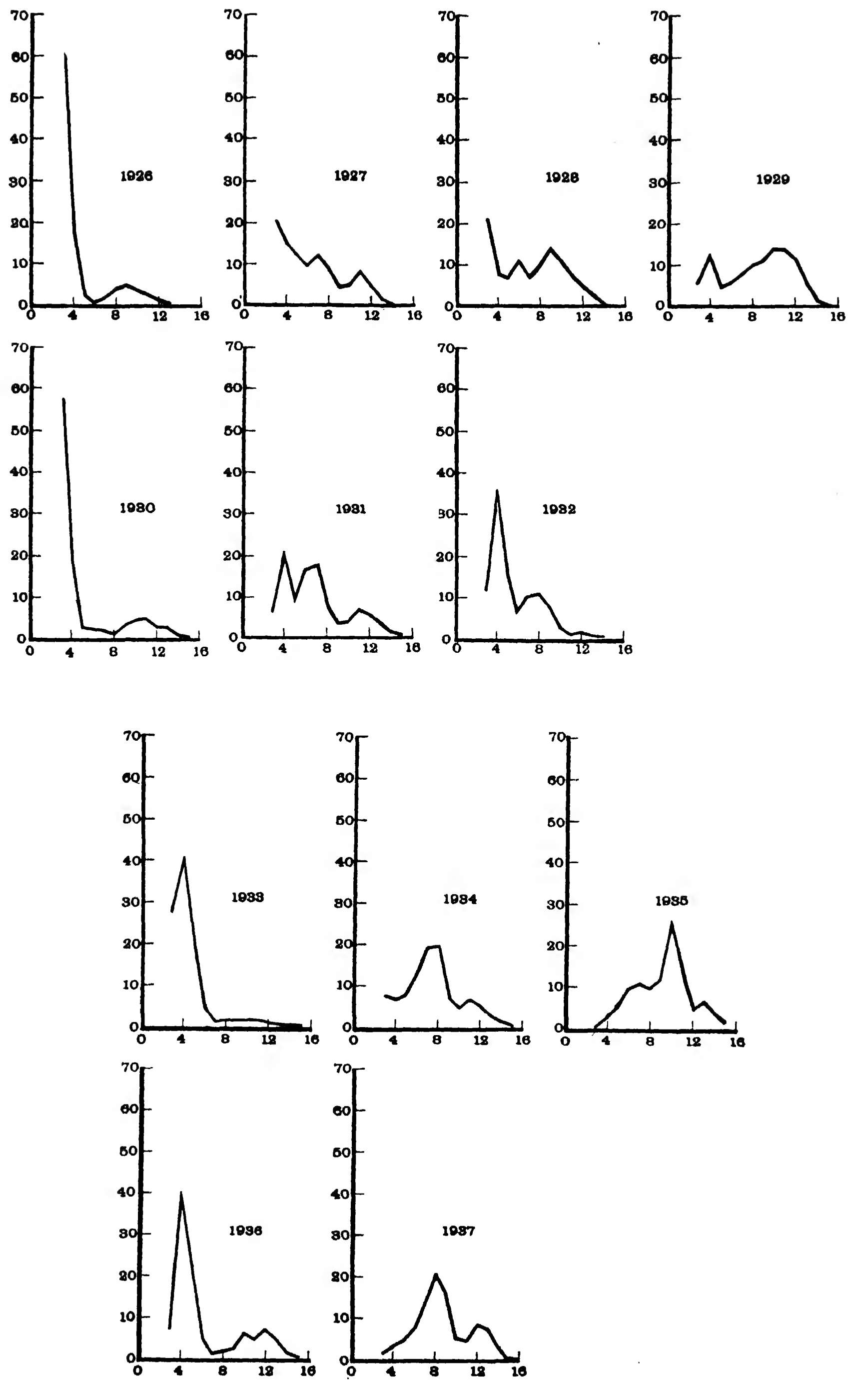


Fig. 1. Figure showing the size-frequency curves for the population of *Tellina tenuis* at low-water mark (station 5), Kames Bay, in the autumn of each year. *Ordinate*, % of total catch; *abscissa*, size in mm.

1925 to 1937 and their possible relation to the broods of *T. tenuis* in Kames Bay during the period. Observations have also been made on *T. fabula* in the same bay and the results are included for comparison with those of *T. tenuis*.

While the observations have been conducted since 1926 it is realized that a much longer period is necessary in such an investigation before thoroughly satisfactory comparisons can be drawn. Owing to the importance of the subject, however, it may be of general interest to summarize the relations so far observed and in the hope that other workers may be interested in testing out what, at the moment, seems to be a reasonable working hypothesis to account for the appearance of large successful broods, at least in intertidal Lamellibranchs.

My thanks are due to Major A. H. R. Goldie of the Meteorological Office, Air Ministry, for supplying me with the weather records and for his help in other ways; also to Mr R. Elmhirst, Director of the Millport Marine Biological Station, for his assistance during my visits to the station where most of this work was done.

2. *TELLINA TENUIS*

(*a*) *General observations*

The principal observations on the size, frequency and density of the population of *T. tenuis* have been carried out in Kames Bay, Millport, where set stations at 40 yd. intervals have been sampled regularly. These stations are numbered from 1 at high-water mark to 5 at low-water mark, and 7 in $2\frac{1}{2}$ fathoms. At low water of spring tides an intertidal area of about 160 yd. in width is exposed. The sand therein is very fine and its texture and water-content is practically the same at all levels.

T. tenuis abounds in the bay, especially at station 5 where the principal observations have been made. This station lies in the centre of the bay at low-water mark of spring tides. The bay has rocks on each side cutting it off from the adjacent sands so that it is a more or less self-contained area. Its extent is thus limited and the spatfalls can be traced fairly easily. This is not the case on the Hunterston sands on the Ayrshire coast opposite, where *T. tenuis* also occurs. But here, owing to the fact that the sands are a mile or more in extent, the spat may settle in different places in different years and a long series of samples would have to be taken to make an accurate estimate of the conditions of the spatfalls. The length of time which could be devoted to sampling in any one year has not been sufficient to cover adequately this area and no attempt is made to compare it with Kames Bay.

At the beginning of the investigation samples were taken at regular intervals during the year; but after some knowledge of the biology of the species had been gained it was seen that this was not necessary, and samples have latterly been taken only in the autumn of each year. On each occasion the same procedure has been adopted. A square of sand with sides 0·5 m. has been marked

out and dug out to a depth of 15 cm., the sand then being run through a sieve with circular perforations 2 mm. in diameter. The measurement of *Tellina* used has been the greatest length, measured to the mm. above. As a rule additional control samples with a finer mesh were taken to ensure that the main collection was an accurate sample of the population.

(*b*) *General history of the population during the period*

The size-frequency curves and the summaries given here refer to the state of the population and the amount of spat in the autumn of each year at station 5 (Fig. 1).

Table 1. *Showing the actual numbers and percentages of the population of* Tellina tenuis *at each mm. length at station 5, Kames Bay, Millport, in the autumn of each year*

	Actual numbers															
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total measured
24 Sept. 1926	508	148	21	5	14	33	39	25	18	8	3	.	.	.	.	822
7 Oct. 1927	158	114	92	71	91	66	31	36	59	34	10	2	.	.	.	764
*28 Sept. 1928	313	114	102	159	103	143	199	159	106	75	38	5	3	.	.	1519
*20 Sept. 1929	59	114	46	53	77	97	104	137	136	112	56	17	4	.	.	1012
27 Aug. 1930	616	197	23	21	19	10	31	43	45	26	24	10	3	.	.	1068
14 Oct. 1931	39	121	56	105	111	45	20	24	39	33	21	8	5	.	.	627
*30 Sept. 1932	56	158	70	29	47	50	35	12	4	5	2	1	.	.	.	469
*3 Oct. 1933	1147	1597	798	178	47	57	65	66	58	42	30	13	7	1	1	4107
24 Oct. 34	64	57	66	111	162	166	60	38	54	43	25	10	4	.	.	860
16 Oct. 1935	1	11	21	39	43	39	47	102	51	19	26	16	8	.	.	423
2 Sept. 1936	84	419	244	55	12	17	24	64	50	77	50	15	2	.	.	1113
4 Oct. 1937	22	40	55	85	158	229	188	62	55	94	87	37	9	3	1	1125

	Percentages														
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
24 Sept. 1926	61·8	17·9	2·5	0·6	1·7	3·9	4·6	3·1	2·2	1·0	0·4	.	.	.	.
7 Oct. 1927	20·7	14·9	12·0	9·3	11·9	8·7	4·1	4·7	7·7	4·5	1·3	0·3	.	.	.
28 Sept. 1928	20·6	7·5	6·7	10·4	6·8	9·4	13·1	10·5	7·0	4·9	2·5	0·3	0·2	.	.
20 Sept. 1929	5·8	11·3	4·6	5·3	7·6	9·6	10·3	13·5	13·4	11·1	5·5	1·7	0·4	.	.
27 Aug. 1930	57·7	18·4	2·2	2·0	1·8	0·9	2·9	4·0	4·1	2·4	2·3	0·9	0·3	.	.
14 Oct. 1931	6·2	19·3	8·9	16·7	17·7	7·2	3·2	3·8	6·2	5·2	3·3	1·3	0·8	.	.
30 Sept. 1932	11·9	33·7	14·9	6·2	10·0	10·6	7·2	2·6	0·9	1·1	0·4	0·2	.	.	.
3 Oct. 1933	27·9	38·9	19·4	4·3	1·1	1·4	1·6	1·6	1·4	1·0	0·8	0·3	0·2	.	.
24 Oct. 1934	7·4	6·6	7·7	12·9	18·8	19·3	7·0	4·4	6·3	5·0	2·9	1·2	0·5	.	.
16 Oct. 1935	0·2	2·6	5·0	9·2	10·2	9·2	11·2	24·2	12·0	4·5	6·1	3·8	1·9	.	.
2 Sept. 1936	7·5	37·7	21·9	4·9	1·0	1·5	2·1	5·7	4·5	6·9	4·5	1·3	0·2	.	.
4 Oct. 1937	1·9	3·6	4·9	7·6	14·0	20·4	16·7	5·5	4·9	8·3	7·7	3·3	0·8	0·3	0·1

* These figures are for $2 \times 0{\cdot}25$ sq. m. In other years the figures are for 0·25 sq. m.

1926. In this year there was a very large amount of brood present on the ground when the samples were taken in September. The brood made up over 60% of the population and had a mode of 3 mm. There was only one other group showing in the graph, namely, an older one with a mode of 9 mm. In the light of later work it is believed that this was derived from the spat of 1924.

1927. On the graph for this year there were three year-groups showing, namely, the new 1927 brood with the mode at 3 mm., the 1926 brood with the mode at 7 mm., and the 1924 brood with the mode at 11 mm.

1928. On this graph, again, three year-groups were showing, namely, the new 1928 brood with the mode at 3 mm., the 1927 brood with the mode at 6 mm., and the 1926 brood with

the mode at 9 mm., and now quite evidently the dominant year-group. The 1924 brood had now almost, if not entirely, died out.

1929. On this graph only two groups were showing, namely a small one, the new 1929 brood with the mode at 4 mm., and a larger one with the mode at 10–11 mm. This latter is very largely derived from the 1926 brood, but the 1927 brood accounts for the irregularity at about 8 mm. on the graph.

1930. In this year there were again only two groups showing, and the size-frequency curve is almost an exact replica of that of 1926. As in that year the population consisted very largely of the new broods, in this case the 1930 brood, while the year-group derived from 1926 and 1927 spats formed a small group from 8 to 14 mm.

1931. In this year there were three groups in evidence, namely, the new 1931 brood showing as a small group with the mode at 4 mm., the 1930 brood with the mode at 7 mm., and numerically the most important group; and finally the group with the mode at 11 mm. comprising the older year-groups, largely the remains of the 1926 brood.

1932. The principal feature of this curve is the presence of the new large brood, the 1932 brood, with the mode at 4 mm. The next year-group, with mode at 8 mm., has been derived from the 1930 brood and possibly to a very small extent from the 1931 brood, for the 1931 brood seems to have very largely died out. The third group with the mode at 12 mm. is very small and is the last remnants of the year-groups older than 1930.

1933. Again the principal feature of this graph is the large and dominating year-group made up of the new 1933 brood with the mode at 4 mm. The only other group showing is the very small one spreading from 7 to 11 mm., all that is left of the older year-groups.

A comparison of this graph with that of the previous year is very instructive, for it would seem that the large and dominant spats of 1930 and 1931 had almost entirely died out or been eaten out. Another point of interest is that the actual amount of this 1933 spat was by far the largest so far met with and averaged over 1600 per 0·25 sq. m.

1934. The new 1934 brood was very small in amount and the dominant year-group, with mode at 8 mm., was that derived from the rich 1933 brood. The older year-group with mode at 11 mm. mainly derived from the 1930 brood was not very large.

1935. On this graph the 1933 brood still survived as the dominant year-group, with mode at 10 mm. The 1935 brood does not seem to have survived at all since only about a couple of dozen individuals could be referred to it. The 1930 brood still shows as a small group with the mode at 13 mm.

1936. The dominant year-group is the 1936 brood with the mode at 4 mm. The fact that no brood was found in 1935 is reflected in the absence of a definite mode at 7 mm. where this group might have been expected to show. The older year-groups have become very much reduced in numbers, being less than half as numerous as they were in the previous year. There are two other year-groups with modes at 10 and 13 mm. derived from the 1933 and 1932 broods respectively.

1937. There was comparatively little brood on the ground in the autumn of 1937, and the dominant year-group was that with mode at 8 mm., very largely derived from the 1936 brood. The survivors of the broods previous to 1936 still formed a not inconsiderable part of the population being represented by the group with mode at 12 mm.

Thus while there was a certain amount of spat laid down every year at station 5 the years 1926, 1930, 1933 and 1936 stand out as vintage years in which it was not only very much larger in amount than usual but also survived to form dominant year-groups at a later period. It is noticeable that while the 1926 brood survived till its fourth year before being followed by a large new brood, the broods of the years 1930 and 1933 each survived only three summers

before this happened. As will be shown later, the most probable explanation lies in the temperature-values during the period.

(c) *Relation of spatfall to temperature*

There are numerous references in literature to the relationships existing between the spawning of marine animals and temperature, but no attempt seems to have been made to correlate the two over a long period. The ideal temperature readings for such a study of *T. tenuis* would be readings taken at the station where the samples were collected. It was not possible to obtain such a series of readings since only occasional visits could be paid to Millport; neither is a complete set of the local sea temperatures covering the whole period available. This is not so serious a matter as it at first sight seems. Since the position of the station is in the intertidal area the temperatures there will follow very closely the local air temperatures. A complete set of these is available from the meteorological station near Rothesay, a distance from Kames Bay of about six miles as the crow flies.

Table 2. *Table showing the deviations, from the means of the period* 1881–1915, *of the monthly mean air temperatures at Rothesay. The last line of figures is the algebraic sum of the means for the period April to September in each year*

	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937
Jan.	+2·9	+1·6	+1·0	+1·6	−2·5	+1·4	−0·6	+4·3	−0·9	+2·5	+2·2	−1·3	+2·0
Feb.	−0·3	+1·6	+1·0	+1·2	−4·6	−3·1	−1·1	+1·8	−0·3	+2·6	+1·2	−1·6	−0·4
Mar.	+0·3	+1·4	+2·0	−0·2	+2·2	−1·3	−2·6	+0·8	+2·9	−1·0	+2·4	+2·2	−3·6
Apr.	−1·8	+1·6	−1·6	−0·6	−2·6	0·0	−1·0	−3·0	+1·4	−1·6	+0·2	−1·2	+1·2
May	−0·9	−2·2	−0·9	−0·1	−0·3	−0·3	−0·5	−1·2	+0·3	−1·5	+0·3	+0·5	+1·4
June	+0·8	−0·8	−5·1	−4·6	−2·1	−0·1	−3·6	+1·1	+1·5	+0·7	−0·9	+0·3	−1·7
July	+0·8	+1·8	+0·6	−3·0	−1·0	−1·0	−1·4	−0·6	+2·4	+3·1	+0·5	−0·4	−1·0
Aug.	+0·2	+1·0	+0·6	−0·8	−1·5	−0·4	−1·1	+0·6	+1·2	−0·8	+1·3	+0·8	+1·3
Sept.	−3·1	+0·3	−1·8	−1·5	+1·4	−0·1	−1·7	−1·5	+2·3	+0·5	−0·2	+1·8	−0·2
Oct.	+1·1	−3·5	+1·5	+0·5	−1·1	+0·1	−0·3	−1·9	+0·9	+0·3	−0·3	+1·5	+0·7
Nov.	−2·2	−1·1	−0·4	+1·1	+1·1	−1·9	+2·3	+0·2	−0·5	+0·1	+0·1	−0·1	−0·1
Dec.	−2·5	+1·5	−2·9	−0·1	+1·7	+0·7	+3·1	+2·3	−0·4	+4·9	−2·2	+2·1	−1·9
	−4·0	+1·7	−8·2	−10·6	−6·1	−1·9	−9·3	−4·6	+9·1	+0·4	+1·2	+1·8	+1·0

For the purposes of this study of the relation of the growth and spatfalls of *T. tenuis* to temperature, several sets of figures may be used. One may use the actual daily temperatures, the monthly means, or, as has been done here, the deviations of the monthly means from a standard set of means (Table 2). The reason for using these figures is to draw a distinction between fluctuations from year to year in colder and warmer periods. By using the deviations from a standard set of means these differences can be given their proper relative values. The algebraic sum of the deviations of the monthly means from the standard means will show at a glance if any year or part of a year has been warmer or colder than normal. In this account the algebraic sum of the deviations for the period April to September is used, since that is the period of the year at Millport during which *T. tenuis* breeds and grows. The figures for the whole year may equally well be used and show the same general features.

The standard means used in the Meteorological Office for the period from 1925 to 1933 inclusive are based on the figures for the period 1881–1915. Those for the period 1934 onwards are based on the figures for the years 1901–30. As is evident, a uniform set of figures is necessary for our purpose. The deviations in the table for the years from 1934 onwards are those calculated to the means used in the first part of the table, namely those based on the years 1881–1915.

For convenience in the wording of the following paragraphs the algebraic sum of the deviations from the mean in the various tables for temperature, sunshine and rainfall respectively will be referred to as *St*, *Ss* and *Sr*.

St for the months, April to September, for the period 1925–36 is shown graphically in Fig. 2. This graph shows that the general conditions were as follows.

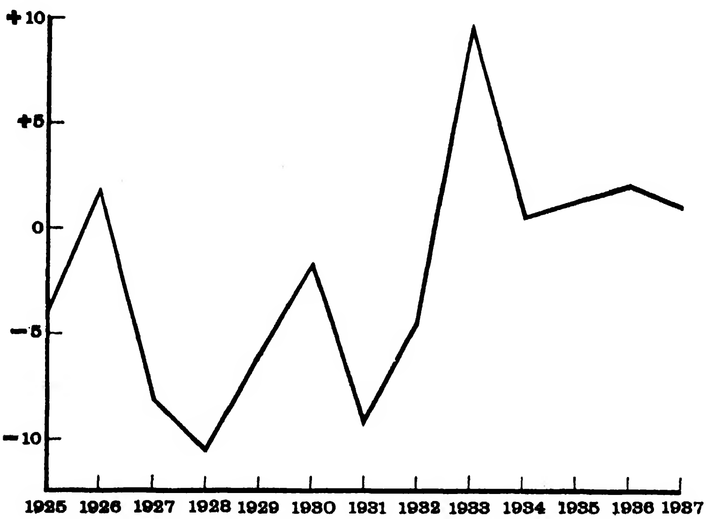


Fig. 2. Figure showing the variations in *St* (the algebraic sum of the deviations of the monthly means of the air temperature from the means of the period 1881–1915) at Rothesay from April to September for the years 1925–37. *Ordinate*, value for *St*; *abscissa*, year.

In 1925 *St* was a fairly low negative value, −4·0, but rose very considerably in 1926 to a positive value, +1·7. In 1927 it fell to −8·2 and in 1928 still lower to −10·6. It rose again in 1929 to −6·1, and still further to −1·9 in 1930. It fell again in 1931 to −9·3 but after that there was a rapid and continuous rise until the peak, +9·1, was reached in 1933. There was a considerable fall in 1934 to +0·4, but after that the figures have been fairly steady being +1·2 in 1935, +1·8 in 1936, and 1·0 in 1937.

Every year a certain amount of brood is found; but in the years intervening between the large broods it has been very much smaller and subject to a heavy mortality.

There seems to be a fairly close connexion between the quantity of the year's brood and the fluctuations in *St*. If, for example, Fig. 3 which shows the actual amount of brood per 0·25 sq. m. in September of each year be compared

with Fig. 2, showing the variation in *St*, it will be seen that the two graphs are very similar indeed. The only discrepancy between the two lies in the figures for 1934 and 1935. A partial explanation of this will be given later.

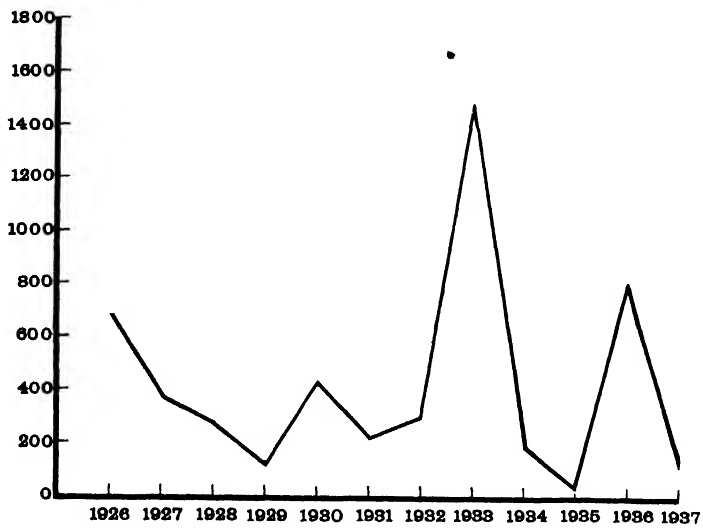


Fig. 3. Figure showing the variations in the actual amount of brood per 0·25 sq. m. in the autumn of each year at low-water mark (station 5), Kames Bay, Millport. *Ordinate*, number of specimens; *abscissa*, year of capture.

Further, the actual extent of the rise in *St* seems to have determined the size of the important broods in 1926, 1930 and 1933. Taking the rise of *St* in 1933 as the basis for temperature and the numbers of brood per 0·25 sq. m. in 1933 as the basis of brood, then the rise in *St* in 1926, 1930 and 1933 is proportional to the quantity of spat produced in these years as shown by the figures below.

Year	No. of spat	%	Rise in *St*	%
1926	675	41	5·7	42
1930	419	25	4·2	31
1933	1660	100	13·7	100

For Lamellibranchs, at least, there is a critical temperature below which a species will not breed. For the American Oyster it is 20° C. (Nelson, 1928). For the European oyster it is 18–20° C. (Spärck, 1935). For the cockle it is 15–16° C. (Orton, 1920). Spärck considers that the large spatfalls of the oyster in Denmark in 1932 and 1934 were due to high temperatures, the average temperatures at Aalborg and Oddesund in July of these years being 17·4 and 18·7° C., and 18·9 and 19·5° C. respectively. These temperatures are somewhat higher than the average temperatures for the Limfjord and approach the temperature of 18–20° C. which is necessary for a considerable renewal of the oyster population. Further, he remarks that if past experience is repeated, this fishery may be renewed for a period, but cannot be expected to last long. If the spatfalls of *T. tenuis* are related to *St*, as I have tried to show that they are,

then for the oyster, too, in all probability until *St* in their locality attains again to a favourable level so long will the oyster spat remain small in amount.

The critical temperature for *T. tenuis* has not yet been determined, but it is noticeable that in the years of the large broods, namely 1926, 1930, 1933 and 1936 *St* approached or went a little above the zero line, Fig. 2. A narrow band lying between +2 and −2 would cover the years 1926, 1930 and 1936. At what point exactly the temperature at the time of spatfall should be marked on the *St* line for 1933 is not now possible to determine, but it probably fell within this band or taking account of the large production of brood just a little above it.

One question arises: if the spatting of *T. tenuis* is conditioned by *St* why was there no large brood in 1934 and 1935, when *St* was at a level which gave a plentiful brood in other years? During the period this has been of two different forms. From 1925 till 1934 it has shown a series of sharp rises and falls; from 1934 till 1937 it has been rather flat and with no very marked variations. During the first period there were three well-defined peaks and these corresponded to the three large broods of *T. tenuis* already mentioned. During the second period there has been one large brood. The correlation during the first period between the position of the peaks on the curve for *St* and the large broods of *Tellina* seem too good to have been the result of coincidence. The appearance of a large brood during the second period where no sharp rise occurred shows that the relationship is still not fully understood, but it is hoped that a further series of observations may throw light on the matter. It is rather remarkable that in spite of the high level of *St* during the period 1935–7, that is in the years before and after the large brood of 1936, that the actual quantity of brood should have been as low as at any time during the whole range of observations.

(*d*) *Relation of spatfall to sunshine*

No records of sunshine are taken at Millport, but figures are available for the total hours of bright sunshine at Rothesay. The deviations of the monthly totals from the means of the period 1914–30 have been obtained from the Meteorological Office and are shown in Table 3. The algebraic sums of these deviations for the months from April to September are shown in Fig. 4.

From this graph it is seen that *Ss* was positive in the years 1925–27, being +34·0, +60·5 and +25·8 respectively, but fell to −44·4 in 1928. It rose again to +48·1 in 1929 but fell to −71·4 in 1930 and to the lowest figure for the period, −180·5 in 1931. From then it rose steadily, becoming positive again in 1935, but since then has been falling. From these figures there would seem to be practically no correlation between the variations in bright sunshine and the spatfalls of *T. tenuis*. The possible exception is the year 1931 when not only was it very sunless, Fig. 5, but also very cold (Figs. 2 and 3). In that year there seems to have been a heavy mortality, especially amongst the young brood which at first was fairly abundant.

Table 3. *Table showing the deviations of the total hours of bright sunshine at Rothesay from the means of the period* 1914–30. *The last line of figures is the algebraic sum of the means for the period April to September in each year*

	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937
Jan.	–16·8	– 8·7	– 3·0	+ 8·5	+21·6	– 3·1	+11·6	+ 3·2	+15·9	+ 4·4	+10·9	+ 9·3	– 8
Feb.	–10·8	–14·2	– 7·0	+15·3	– 6·2	+18·8	+ 2·9	+44·1	+25·3	+13·2	+ 8·0	+ 9·1	+19
Mar.	+17·8	–42·1	+16·6	–43·8	+69·8	–17·7	+ 7·5	– 4·3	0·0	–16·8	– 9·3	–64·8	+16
Apr.	+16·8	–28·4	– 3·9	– 8·7	+ 8·5	– 6·9	–21·2	+ 4·0	–62·5	–27·4	– 2·0	–34·5	–87
May	–48·8	– 5·6	+46·1	+22·1	+45·1	+18·8	–16·1	+ 0·3	–34·1	–36·1	+91·4	+16·1	+37
June	+76·6	+ 1·4	+ 1·8	–21·6	+28·1	– 0·2	–99·0	+ 8·6	– 9·3	– 2·2	–54·9	+19·9	–25
July	– 5·5	+51·5	–15·3	–49·1	+ 0·5	–36·8	–76·4	–53·0	– 6·3	+65·5	+42·9	– 5·3	–20
Aug.	–28·9	+29·1	+ 9·8	– 4·8	–26·8	–19·0	+53·0	–24·1	+ 7·9	–24·9	– 7·9	–13·0	+10
Sept.	+23·8	+12·5	–12·7	+17·7	– 7·3	–27·3	–20·8	– 8·4	+50·6	0·0	–13·5	–22·9	+ 8
Oct.	– 1·8	+17·0	+10·7	–12·1	+ 0·8	–19·4	+ 6·7	– 4·6	–23·5	–23·6	–24·5	+ 8·6	0
Nov.	+25·9	0·0	+ 5·3	+ 4·2	–13·8	+ 5·0	–22·2	–11·7	+ 0·1	+ 4·6	– 8·1	–15·6	– ?
Dec.	+ 3·9	+ 1·8	– 0·2	+ 2·9	+ 5·8	– 4·8	–20·2	+ 0·4	–15·4	–26·9	+15·7	–28·8	+11
	+34·0	+60·5	+25·8	–44·4	+48·1	–71·4	–180·5	–72·6	–53·7	–25·1	+56·0	–39·7	–77

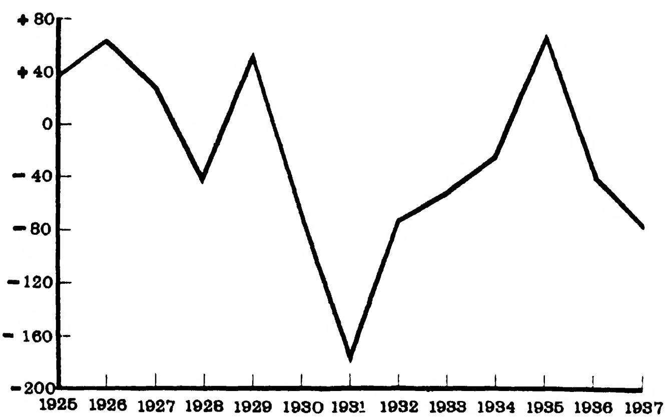


Fig. 4. Figure showing the variations in *Ss* (the algebraic sum of the deviations of the monthly total hours of bright sunshine from the means of the period 1914–30) at Rothesay from April to September for the years 1925–37. *Ordinate*, value for *Ss*; *abscissa*, year.

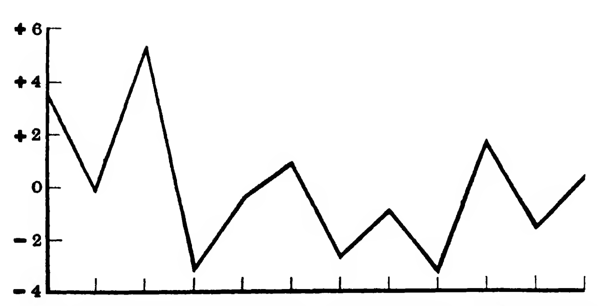


Fig. 5. Figure showing the variations in *Sr* (deviations of the monthly totals of rainfall from the means of the period 1925–35) at Millport from April to September for the years 1925–36. *Ordinate*, value for *Sr*; *abscissa*, year.

(*e*) *Relation of spatfall to rainfall*

Readings of the local rainfall are taken at the Millport Station and for the purposes of this paragraph the monthly totals in inches have been used. No figures for standard monthly means are issued by the Meteorological Office, so the means for the years 1925–35 have been calculated. The deviations of the monthly totals from these means are shown in Table 4 and the algebraic sum of the deviations for the months April to September are shown graphically in Fig. 5. An examination of these shows that there is no correlation between the local rainfall and the fluctuations in the amounts of the broods of *T. tenuis*. In the years of the big broods, for example, 1926, 1930, 1933 and 1936, while *Sr* was almost at zero in 1926 and 1936 and but little above it in 1930 it was actually at its lowest value in 1933.

Table 4. *Table showing the deviations of the monthly totals of rainfall in inches at Millport from the means of the period* 1925–35. *The last line of figures is the algebraic sum of the means for the period April to September in each year*

	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
Jan.	−0·59	+1·40	+1·22	+4·58	−3·47	−0·04	−0·49	+0·66	−0·93	−0·10	−2·21	−1·50
Feb.	+0·89	+1·82	−0·15	+1·47	−0·30	−2·50	+1·19	−2·72	+0·21	−2·36	+2·47	−0·77
Mar.	−0·56	+0·78	+1·47	+1·98	−1·15	−0·04	−1·47	−0·05	−0·47	−0·22	−0·29	+0·69
Apr.	+2·82	−0·32	+0·40	−1·03	−1·63	−0·47	−0·78	+1·30	−0·65	−0·05	+0·37	−1·22
May	+3·51	−0·15	−0·15	−1·55	+0·79	−0·62	+0·89	−0·70	−0·30	+0·25	−2·01	−0·15
June	−2·23	−0·01	+2·17	+0·93	−0·14	+0·20	+1·13	−1·21	−0·52	−0·47	+0·11	−1·28
July	−0·97	−0·27	+0·63	−0·87	+0·21	−0·31	+0·94	+0·50	+0·91	−0·02	−0·73	+2·68
Aug.	+0·30	+0·50	+0·07	−0·41	+2·43	+1·97	−2·72	−0·14	+0·01	−0·24	−1·82	−0·30
Sept.	−0·01	+0·08	+2·33	−0·16	−2·17	+0·04	−2·20	+0·56	−2·82	+2·03	+2·38	+0·47
Oct.	−1·52	+0·88	−1·48	+2·90	−0·65	+0·43	−2·12	+0·19	−2·97	+0·85	+3·52	−1·06
Nov.	−3·41	+2·45	+0·51	+1·48	+2·46	+0·31	+2·73	−1·15	−1·73	−3·71	+0·55	−1·62
Dec.	−1·73	−2·35	−3·72	−0·28	+6·53	+0·78	+0·70	+2·53	−2·83	+3·23	−1·41	+1·91
	+3·42	−0·17	+5·05	−3·19	−0·51	+0·81	−2·74	−0·99	−3·37	+1·50	−1·70	+0·20

3. *Tellina fabula*

Relation of spatfall to temperature

This species is also common in Kames Bay where it lives in the sandy area extending from close to low-water mark of spring tides out to the middle of the bay. Samples have been taken in September of most years since 1926, the station worked being about 50 yd. seawards of station 5 where the depth is 2½ fathoms. The size-frequency curves for these collections are shown in Table 5, Fig. 6, for comparison with those of *T. tenuis*. It must be remembered, however, that not quite the same reliance can be placed on them for giving an accurate sample of the population, and that for two reasons. In the first place the collections were taken with a dredge and one cannot be quite certain that all the older and larger individuals were captured, some may have been below the working level of the dredge. In the second place Kames Bay is a feeding ground for several species of fishes, and examinations of stomach contents has shown that *Tellina* is consumed in quantity. This will reduce the

Table 5. *Showing the actual numbers and percentages of the population of* T. fabula *at each mm. length at stations* 6 *and* 7, *Kames Bay, Millport, in the autumn of each year*

Actual numbers

	3	4	5	6	7	8	9	10	11	12	13	14	Total measured
*2 Feb. 1931	83	691	424	90	17	4	22	16	3	3	.	.	1353
28 Oct. 1931	5	54	103	54	68	138	86	23	8	6	1	.	546
1 Oct. 1932	1	4	15	5	4	3	12	26	16	8	2	.	96
4 Oct. 1933	131	632	526	89	17	10	18	39	49	14	3	1	1529
24 Oct. 1934	30	55	8	3	17	28	29	4	9	6	1	.	190
23 Sept. 1935	117	392	179	28	3	3	12	12	13	4	.	.	763
5 Sept. 1936	6	65	17	8	17	24	32	18	21	7	2	.	217
4 Oct. 1937	44	30	17	10	10	25	50	51	31	33	11	1	313

Percentages

	3	4	5	6	7	8	9	10	11	12	13	14
*2 Feb. 1931	6·1	50·7	31·1	6·6	1·2	0·3	1·6	1·2	0·9	0·2	.	.
28 Oct. 1931	0·9	9·9	18·9	9·9	12·4	25·2	15·7	4·2	1·5	1·1	0·2	.
1 Oct. 1932	1·0	4·2	15·6	5·2	4·2	3·1	12·5	27·1	16·6	8·3	2·1	.
4 Oct. 1933	8·6	41·3	34·4	5·8	1·1	0·7	1·2	2·6	3·2	0·9	0·2	.
24 Oct. 1934	15·6	29·0	4·2	1·6	9·0	14·7	15·3	2·1	4·7	3·2	0·5	.
23 Sept. 1935	15·3	51·3	23·4	3·7	0·4	0·4	1·6	1·6	1·7	0·5	.	.
5 Sept. 1936	2·8	29·9	7·8	3·7	7·9	11·0	14·7	8·3	9·7	3·2	0·9	.
4 Oct. 1937	14·0	9·6	5·4	3·2	3·2	8·0	16·0	16·3	9·8	10·5	3·5	0·3

* Since there is no growth over the winter months these figures are taken as representing the autumn collection of 1930.

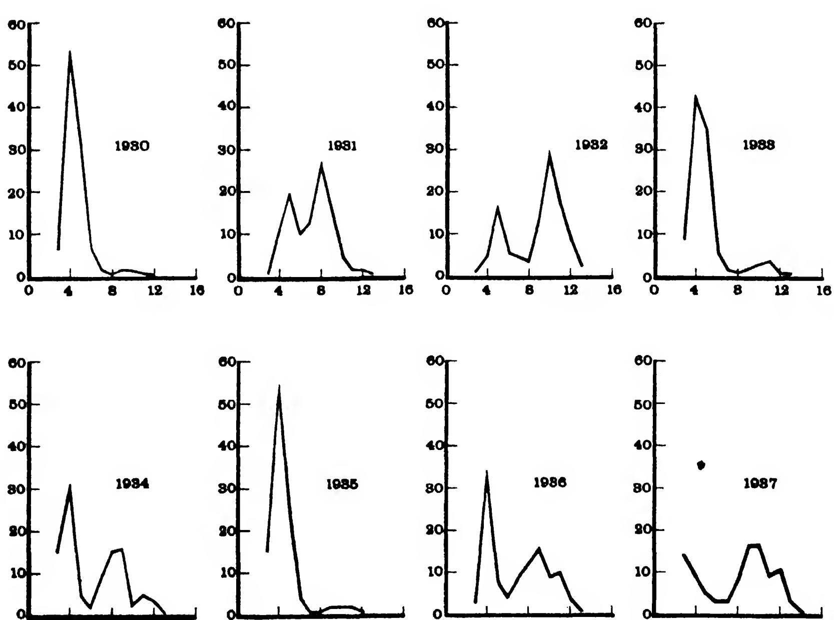


Fig. 6. Figure showing the size-frequency of the population of *Tellina fabula* at a depth of 2½ fathoms (station 7), Kames Bay, in the autumn of each year. *Ordinate*, % of total catch; *abscissa*, size in mm.

numbers of the older groups and tend to make the proportion of brood higher than it would be in an undisturbed population, a point to bear in mind when considering the size-frequency curves. No collection was made in September 1930 but one was made in February 1931 and it may be used instead as there is no growth over the winter and the population remains stationary.

Taking 6 mm. as an arbitrary figure to indicate the limit of the growth of the brood in the autumn of each year, then the proportion of the brood to the total catch in September of each year was as shown in the following table.

Year	% of spat	Year	% of spat
1926	92·9	1934	50·4
1930	94·5	1935	93·7
1931	39·6	1936	44·2
1932	26·0	1937	32·2
1933	90·1		

Making allowances for the two sources of error already mentioned, it would still seem that in the years 1926, 1930, 1933 and 1935 large broods of *T. fabula* occurred. The years 1926, 1930, 1933 and 1936 were the years of the large broods of *T. tenuis*, so that the two species coincide except for the last year. It has already been shown that there was a large drop in *St* from 1933 to 1934 and that might explain why there were no large broods in that year in spite of the fact that *St* remained positive. There is no such reason as to why there was no large brood of *T. tenuis* in 1935, when there was a slight rise in *St* and when one might have been expected. It is important to note that there was one for *T. fabula* in 1935. On the other hand, there was no large brood of *T. fabula* in 1936 although there was one of *T. tenuis*. Only further observations can solve the problem, but at this stage it would seem that, as already suggested, when the changes in *St* are sharp, upwards, large and reach a certain figure, then large broods follow. When, as has been the case since 1932, *St* has remained fairly high without showing sharp fluctuations, large spats will come during that period but not every year nor, as in the case of the two species of *Tellina*, in the same year.

4. Summary

1. This paper deals with the possible correlation between the broods of *Tellina tenuis* and *T. fabula* in Kames Bay Millport, and temperature, sunshine and rainfall. The two species occur in the area of the littoral and sublittoral influences, respectively.

2. While some brood is found every year, the years 1926, 1930, 1933 and 1936 were marked by very large broods of *T. tenuis*.

3. There is apparently a close relation between the occurrence of these spats and the temperature in most years. The algebraic sum of the deviations of the monthly means from a standard set of means (*St*) for the period April to September of each year shows sharp rises in the years 1926, 1930 and 1933.

4. The quantity of brood seems to be proportional to the rise in *St*.

5. There seems to be practically no relation between sunshine and these years of large broods in *T. tenuis*.

6. There seems to be no relation between the rainfall and these years of large broods in *T. tenuis*.

7. The years of the large broods of *T. fabula* have been the same as those for *T. tenuis* (1926, 1930 and 1933) except in the period when *St* was high and fairly steady when it came the year before, 1935 instead of 1936.

REFERENCES

Nelson, T. C. (1928). "Relation of spawning of the oyster to temperature." Ecology, 9: 145–54.

Orton, J. H. (1920). "Sea-temperature, breeding and distribution in marine animals." J. Mar. Biol. Ass. U.K. 12: 339–66.

Spärck, R. (1935). "Investigations on the biology of the oyster." Rep. Danish Biol. Sta. 40: 39.

A SURVEY OF THE VERTEBRATE FAUNA OF THE ISLE OF MAY (FIRTH OF FORTH)

By H. N. SOUTHERN

(*With* 1 *Map*)

CONTENTS

A. NOTE ON THE HOUSE MOUSE (*MUS MUSCULUS*)

Twelve examples of *Mus musculus* L. were trapped on the Isle of May during July 1936. Ordinary break-back traps were used and these were set at night and visited in the early morning, and during the following day. The interval that must have occurred between trapping and collecting in many cases probably accounts for the small number of fleas (Siphonaptera) recorded. In one of the two cases where they were found the individual was still alive in the trap. Many mites (Acarina) were collected from some of the specimens. All these belonged to the species *Aleurobius farinae* Koch, and had evidently come from the storehouses that the mice frequented.

Trapping was first carried out in the outhouses and stores of the lighthouse buildings; but since only small numbers were obtained in this way, the walls of the various enclosed fields were tried, with a much higher yield. Towards the end of the visit, however, a period of wet weather intervened, and most were then caught again in the outhouses.

The Isle of May is five miles distant from the nearest coast (that of Fife to the north). The rest of the mammal fauna consists entirely of rabbits (*Oryctolagus cuniculus* L.). The lighthouse keepers are certain that there are no rats, and trapping along the rocks near the coast produced no shrews.

I wish very gratefully to acknowledge the help given me in identification by the following experts: Dr H. A. Baylis (parasitic worms); Mr F. J. Cox (Siphonaptera); and Mrs Margaret Hughes (Acarina).

Table of weights, measurements, parasitization

Specimen	Sex	Date (July)	Wt. (g.)	Body plus tail length (mm.)	Tail length (mm.)	Ectoparasites	Endoparasites	Remarks
1	♂	11	23·75	175	80	Many mites (see above)	None	Brought in dead, not examined till 12 hr. since death
2	♂	11	18·5	155	72	None	3 nematodes (*Trichurus muris* Schrank)	Examined very soon after death
3	♀	12	26·0	159	75	Many mites	5 nematodes in caecum	Examined following morning. Four embryos weighing 3·5 g. deducted from weight
4	♂	17	18·5	145	66	Many mites	None	Examined following morning
5	♀	18	24·0	169	75	Many mites	4 nematodes in caecum	Examined following morning
6	♂	22	17·0	154	70	Many mites, 1 flea (*Nosopsyllus fasciatus* Bose)	2 nematodes in caecum	Examined about 12 hr. after death
7	♂	22	16·0	144	65	Many mites	None	Found as above
8	♂	22	24·0	156	75	Few mites	None	Examined following morning
9	♂	22	16·0	145	74	None	1 nematode in caecum	As above
10	♂	22	23·5	165	75	None	None	Examined shortly after death. Cestode cyst (? sp.) in liver
11	♂	23	18·5	155	75	1 mite	1 nematode in caecum	Examined following morning
12	♂	23	10·0	125	65	No mites, 3 fleas (*Nosopsyllus fasciatus*)	None	Caught alive, examined at once

B. CENSUS OF BREEDING BIRDS

1. Scope of the survey

The census was carried out under certain difficulties which made it impossible to achieve as great a completeness as is desirable. In the first place the work was done during the period, 2–26 July, when a number of the resident Passerines had finished breeding, and it was only possible to make a rough estimate of the pairs present by judging from the total of birds seen, including fledged young. Secondly, all observations were made by the author alone with the consequent difficulty of covering much ground at a time. Finally, it was not feasible to make more than an estimate of the cliff populations, though the methods adopted should have given a certain degree of accuracy.

The aim of the enquiry was not to make a complete biological survey, though a vegetational map was made with the help of another member of the party, and where such environmental factors are thought to have had an effect upon the distribution of the birds, they are mentioned. The two main objects in view were (*a*) to estimate the population of the resident Passerines to give a criterion for judging the influx of migrants of the same species, and (*b*) to estimate the total strength of the breeding birds of all kinds to afford a basis of comparison for previous and subsequent work of a similar nature.

2. Methods adopted

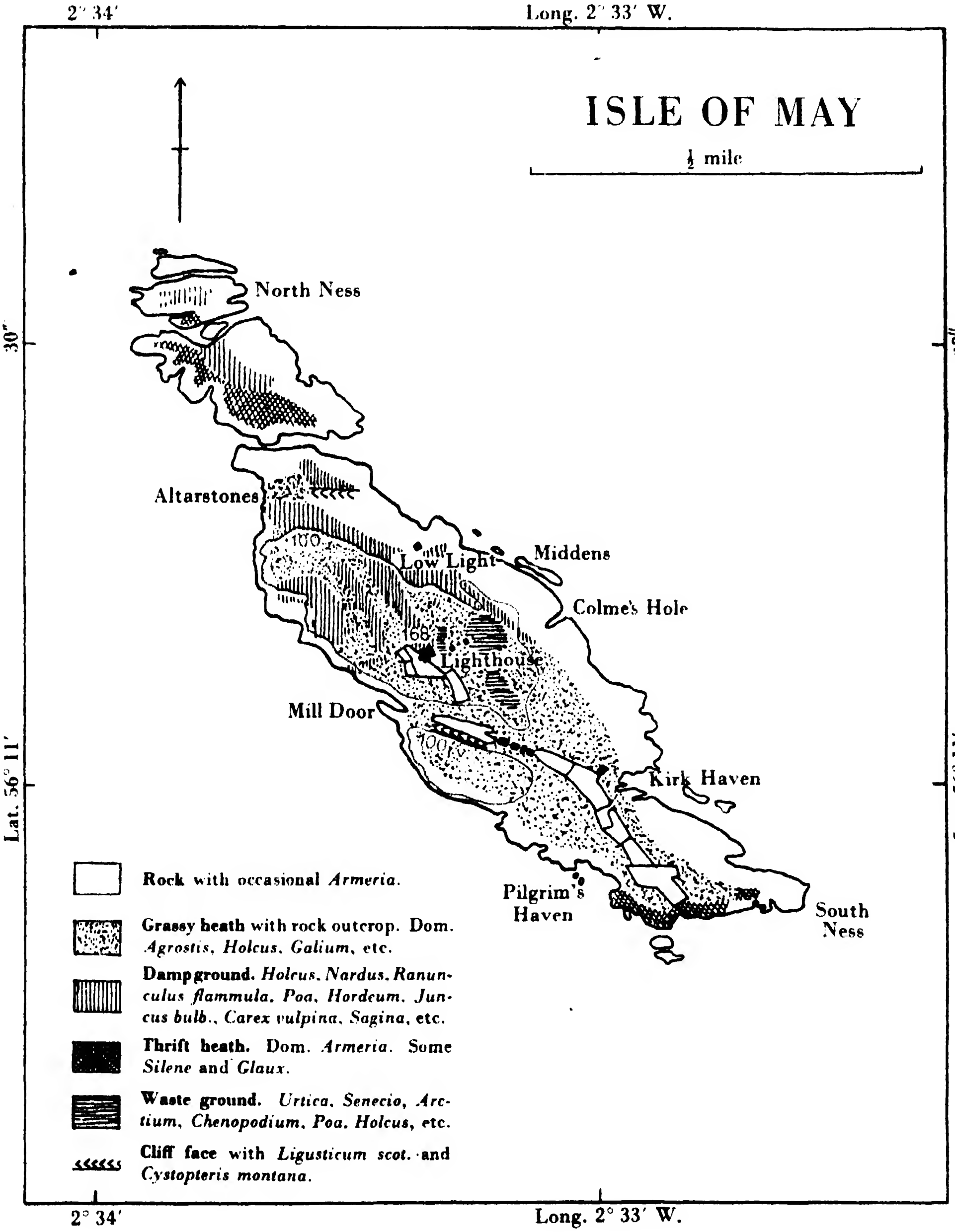
The aim in every case was to count the total population of the birds and not to rely upon sample areas, with the single exception of the ternery, where the calculation was straightforward owing to their even distribution. In the case of the rock pipits, practically all the adults were still holding territory in the earlier part of July, so that a circuit of the coast gave the required information. The blackbirds and song thrushes still remained more or less in their original territories with their fledged young during the first week, and the same applied to the pied wagtails and to the meadow pipits, but the starlings and house sparrows gave more difficulty. After about a fortnight the birds of the year of both species formed two self-contained flocks, so that a rough estimate of the pairs likely to produce so many young could be arrived at.

Worst of all were the wheatears and eiders: the former were in heavy moult and kept out of the way, while the eiders had practically all hatched their families, and the drakes had disappeared, with the exception of two birds in very black plumage. However, none of the young appeared to be very old, and it is possible that the count of families taken represents fairly accurately the number of pairs nesting, with the exception of unsuccessful ones. None of the families had combined at that time.

The oyster-catchers and lesser black-backed gulls presented little difficulty on account of the smallness of their numbers; while the herring gulls only required a little patience, since they were concentrated at two focal points,

with a sprinkling round the rest of the coast that could easily be counted by a circuit.

In the case of the cliff birds the job was rather laborious but by no means impossible. The actual methods varied with the species: with the fulmars and



shags it was a case of marking down each nest from the cliff tops and then checking them from the sea; adding such as had been missed on account of overhangs, clefts, etc. The kittiwakes were most easily estimated by counting

the nests from the seaward side; while in the case of the guillemots and razorbills an attempt was made to count the actual parent birds.

It was impossible to distinguish the two species from a rocking boat, so a count was first taken of the total of both kinds actually on the cliffs. Later a count was taken at the same time of day and under the same weather conditions from the cliff tops of the birds on the water, and the proportion of razorbills to guillemots carefully noted. The same proportion was applied to the previous count on the cliffs and the totals added together. Puffins presented obvious difficulties on account of their hole nesting habits; but a similar count was taken including both birds on the water and on the cliffs. A further addition of about 40 % of this total for incubating birds seems not unreasonable.

The procedure at the ternery was almost rule of thumb. About eight sample squares of ground in all parts of the ternery were marked out, measuring 20 by 20 yd. (i.e. 400 sq. yd.) and the number of nests in each carefully counted. It was found that these samples fell fairly distinctly into three classes, of which one averaged 80 nests, the second 45 nests, and the third 30 nests. There were only two foci with the very dense population, while the majority of the ground fell into the second class, the third composing the outlying areas. Thus it was possible by pacing out the whole extent of the ternery, and making the necessary allowances for the small areas of greatest and least density to arrive at an accurate idea of the total number of nests. From this datum it was easy to separate off the Sandwich terns on account of their small numbers. Towards the end of the month the author was assisted by Mr Frank Elder to count the number of arctic terns, thus completing the whole survey.

3. General topography and the main communities

The Isle of May is about 1½ miles long and ¼ mile broad and its long axis is orientated slightly west of north and east of south. The rock is basalt, forming sheer cliffs about 100 ft. high on the west side, and either low cliffs or irregular rocky terraces and slopes on the east side. The northern part of the island is cut off from the rest at high tide. It consists of low, uneven ground and is occupied chiefly by the terns. The main part of the island is grooved in a north-west to south-east direction by a valley that provides some shelter.

With the exception of the North Ness, which has sparse vegetation with *Rumex* and *Silene*, the major part of the island consists of a rough turfy surface characterized chiefly by *Holcus*, *Agrostis*, *Nardus*, *Galium*, *Cerastium*, *Potentilla*, etc., with frequent outcrops of rock. Practically the whole circumference is covered with dominant *Armeria*, which extends even along the west side of the North Ness.

The presence of man has two aspects: the occupation of the valley with the construction of a fresh-water loch at the north-west end, and the walling in of certain areas to form enclosures, of which the trapping garden is one. Here an

abundance of weeds has settled. The other effect of man's presence is the large cap of cinders and coal dust deposited on top of the island near the old beacon, which has been captured by *Urtica*, *Carduus*, *Arctium*, *Chenopodium*, *Ranunculus*, *Poa*, etc. From this centre other patches have been colonized by these plants.

Of mammals living on the island there are only two and by far the more important is the rabbit (*Oryctolagus cuniculus*), which swarms all over it. By its agency the turf is kept close cropped, and the burrows may offer retreats to some puffins, wheatears, etc. No doubt rabbits also provide a certain amount of food for the gulls. The resident house mouse (*Mus musculus*) is of the large insular variety found on many islands round the British Isles, and is confined in its distribution to the valley. Trapping along the rocks failed to produce any shrews and apparently there are no rats on the island.

The insect population is fairly varied and was studied by another member of the party, Mr H. G. Callan, who will publish his results in due course.

The birds may be divided roughly into the following communities: (*a*) the small Passerines that occupy the greater part of the island and get their food from it; (*b*) birds that nest and feed along the shore, represented only by the oyster-catcher; (*c*) birds that use the island only for nesting and occupy the cliffs or the other margins and the North Ness; and (*d*) half-way birds that nest along the margins or a little way above them and get some of their food from the island. It is under these headings that the figures will now be considered.

4. Census results

(*a*) *Passerines*

Rock pipit (*Anthus spinoletta petrosus*). 24 pairs. This is perhaps the most characteristic bird of the island. Its distribution is fairly even all round the margin, with some concentration along the East Rocks. The cove known as Colme's Hole was such a satisfactory habitat that two pairs were breeding in it, the nests being not more than a dozen yards apart. One nest had newly hatched young on 12 July, though they were subsequently deserted upon the establishment of a roost of first-brood young in the cleft concerned.[1] The two other nests found both had young in much later stages of development. All had a high proportion of unfertile eggs, which may indicate exhaustion of the reproductive organs in such late broods. The first-brood young ranged all over the top of the island as well as the margins and frequently fed in the waste patches of ground near the Observatory. Birds were also found roosting in company in patches of nettles, and in rock clefts, as noted above.

Meadow pipit (*Anthus pratensis*). 2 pairs. This species showed a constant difference in habitat selection from the foregoing. During the first week they were seen ranging over the turfy ground on top of the island, and after that they seemed to feed for the greater part in and around the sheltered fields in the valley.

Wheatear (*Oenanthe oe. oenanthe*). 3 pairs. Very difficult to assess correctly. However since three of the birds seen were probably cocks, though disguised in heavy moult, and twelve birds in all were seen, the figure seems not unreasonable. These again were distributed much in the same way as the meadow pipits except that they preferred the ground with more rock outcrop.

[1] For further notes on this subject, see **Southern, H. N.** (1937). Brit. Birds, 29: 2.

The three preceding species might be called the truly indigenous birds of the Isle of May, since they inhabit the ground that is most typical of it. The following ones are all in some degree invaders, probably having arrived in the trail of man.

Starling (*Sturnus v. vulgaris*). 6 pairs. There may possibly have been a previous indigenous stock of these birds on the island nesting in rabbit holes, crannies in the cliff, etc.; but this seems unlikely in view of the history of the starling in the surrounding region of Scotland (**1**). It has more probably spread to the island contemporaneously with its increase on the mainland. Starlings were principally to be seen round the premises of the lighthouse keepers and various derelict buildings with their fledged broods, though they covered the whole island in their foraging sporadically, even working the North Ness. The family parties were observed later to be joined up into one flock.

House sparrow (*Passer d. domesticus*). 6 pairs. Naturally this species is even more confined than the starling to the buildings, and most of them inhabit the valley, though one female was seen at the Low Light. The young birds had formed a flock of about 20 by the third week and were to be seen mostly in the fields and gardens. Many were trapped and found to be infested by a bird fly (*Ornithomyia fringillina* Curtis) to the extent of half a dozen to each individual. As many as ten were produced by one unfortunate.

British song thrush (*Turdus e. ericetorum*). 2 pairs. One pair of these birds lived in the valley; but the other occupied the part of Holyman's Road near the Low Light (where the slight dip gives some shelter), being thus independent of man.

Blackbird (*Turdus m. merula*). 3 pairs. These were confined to the valley and to the lighthouse gardens for breeding, though odd birds hunted somewhat further afield. A favourite place for one male was in the waste patch round the Observatory.

Pied wagtail (*Motacilla alba yarrellii*). 2 pairs. This species is perhaps not quite so dependent upon man as the four previously mentioned, but one pair with fledged young was continually seen round the fresh-water loch, and the lighthouse grounds nearby, while the other pair frequented the lower fields near the Priory. These again fed over a wider area sporadically, being encountered round the Observatory and on the ground between the East Rocks and the valley.

This completes the list of the Passerines. Fortunately no complications due to migrant birds were introduced, so the total given (48 pairs) is a pretty fair estimate of the real population. It is to be noticed that the rock pipit is the bird really characteristic of this community, and all the others are living rather near the danger margin as regards numbers.

(*b*) *Shore birds*

Oyster-catcher (*Haematopus ostralegus occidentalis*). 7 pairs. The formation of the shoreline does not encourage a large population of shore birds, and it is interesting to find that only this species has managed to establish itself. The individual pairs are scattered fairly well round the island, and for the most part keep to the low broken rocks such as those at the North and South Ness. An exception however is a pair that was constantly seen on top of the cliffs just behind the fresh-water loch. Two nests were found, one of which still contained eggs on 25 July.

(*c*) *Cliff birds and the ternery*

(The eider is included in this category, as being a bird that feeds at sea, and merely uses the land to nest.)

Kittiwake (*Rissa t. tridactyla*). 2950 pairs. The most abundant of the cliff community, preferring the higher and more perpendicular cliffs from 50 to 100 ft. high. On such a formation as this, where the basalt tends to split and leave platforms rather than continuous ledges the nests are often disposed in an inverted V-shape, which would give the maximum crowding without any of the nests being over one another. It can easily be seen by observing the way in which the cliffs are "whitewashed", that the kittiwake prefers to nest under an overhang or under a small jutting "umbrella" of rock. In this way their plumage is kept clean in sharp contradistinction to that of the guillemots. Wherever there was the slightest chance it was noticeable that these birds strung themselves in typical single lines.

A count was taken one morning to get an idea of the rate of chick survival. The figures must be taken as the maximum, for some of the nests had eggs still; in most cases however the young were fairly large and had a reasonable chance of being fledged. No. of nests with 2 *young (or eggs)*, 50; 1 *young (or egg)*, 28; *no young (or eggs)*, 10.

Northern guillemot (*Uria a. aalge*). 2080 pairs. The formation of the rocks did not allow these birds to crowd together in their usual hordes, and they were for the most part distributed in groups of a score or so on each platform. In this way there was not so much communism in the care of eggs and young as at some of the larger colonies. In some places, owing to the stepped formation of the basalt, birds were nesting much lower down the cliffs than is usual, and in flying off they usually bounced off the water once or twice before they could get under way.

The cliffs were carefully examined under all possible light conditions, and it seemed certain that there was a small admixture of the southern form, as would be natural so close to the edge of its range.

A count was taken on all the cliff faces as far as the Mill Door from the direction of the Angel to determine the proportion of the "ringed" variety from as large a figure as possible. In all 1468 were counted, of which 72 were ringed, giving a proportion of just over 5%. Only in one instance were two ringed birds seen to be mated together.

Razorbill (*Alca torda britannica*). 500 pairs. These birds occupied much the same area as the guillemots except that they spread out further on to the lower and more broken-up cliffs.

Puffin (*Fratercula arctica grabae*). ? 50 pairs. A superficial count gives the impression that puffins are very few on the island, but there is little reason to doubt the figure given, as explained above. They inhabited the topmost parts of the cliffs, and the majority of them occurred on the cliffs between the Mill Door and the West Landing.

Shag (*Phalacrocorax a. aristotelis*). 10 pairs. These birds hide themselves away so efficiently in cracks and caves that they are not easy to count. In addition the immature birds that hang about have to be carefully distinguished from the breeding adults. One crevice was found which contained a small colony of three nests, and the rest were distributed along the lower portion of the more precipitous cliffs.

Fulmar (*Fulmarus g. glacialis*). 4 pairs. These were split up into two groups of two, one nesting upon ordinary broken cliff and the other upon a face sufficiently out of the perpendicular for rough grass and turf to cover it. Incubation was still going on.

Eider (*Somateria m. mollissima*). 32 pairs. As explained, this figure is based upon the actual number of families seen. In addition 37 other ducks were seen either singly or in groups, but with no ducklings. Most of these were distributed round the North Ness, the South Ness and the east side. One bird was still sitting in among the gulls on the rock known as the Maiden's Hair. Most of the old nests appeared to be just above the rocks in the belt of thrift. Families averaged about three ducklings.

Common tern (*Sterna h. hirundo*). 3400 pairs. Practically all were nesting on the North Ness with the exception of two pairs on the East Rocks not far from Kirk Haven. The body of them occupied the peaty ground in between the rock pools among the *Rumex* vegetation and the somewhat higher *Armeria*-covered ground on the west side of the North Ness. The

two foci of densest population were, curiously, some way apart from the others, one being on the rocks just above the Tarpot, the other one the single patch of shingle near Norman Rock. Each of these contained about 200 nests.

Arctic tern (*Sterna macrura*). 800 pairs. These kept in a compact body on the bare rocky ground to the east and south of the common terns.

Sandwich tern (*Sterna s. sandvickensis*). 4 pairs. These nested in among the common terns, and it was observed that although they kept together in a group, they were molested by their neighbours every time they attempted to approach their nests. One by one the eggs were found broken and sucked, and finally the birds gave up the attempt to breed.

It is as well to mention in view of the curious desertion of the colony that took place later that all the terns were still there on 26 July, most of them having chicks about a week old.

(*d*) *Partly predatory species*

Herring gull (*Larus a. argentatus*). 455 pairs. The two main colonies of these were on outlying rocks, one being the Middens on the east side and the other the Maiden's Hair rock not far from the foghorn. In addition they nested on the South Ness and all along the top of the rocks from there to the beginning of the higher cliffs, and then again in rather scattered pairs on the west side of the North Ness. In every instance they prefer to nest on the actual rocky edge of the cliff or a little way down it. Most of the young birds caught for ringing purposes disgorged small fish, but no doubt the adults feed upon rabbits and eggs a good deal.

British lesser black-backed gull (*Larus fuscus affinis*). 7 pairs. Only one of these pairs nested on the Middens, the others preferring the turfy slopes near the foghorn, just above the line of the cliffs where the herring gulls lived. Even when in such small numbers their habitat selection holds good.

5. Non-breeding birds

As far as could be ascertained there were very few of these, except in the case of the gulls. There was usually a flock of anything up to 200 immature and mature birds to be seen either on the South Ness or on the Norman Rock at the North Ness. The majority was coming into adult plumage and had only a little brown in the wings and a band across the tail. Most of these were herring gulls, though perhaps half a dozen were lesser black-backs. On 20 July, 11 mature and 9 immature greater black-backed gulls (*Larus marinus*) were seen with this flock on the Norman Rock. It is difficult to classify them exactly, since the presence of the mature birds may point to the beginning of a migratory movement.

There were always some shags around the coast, and a congregation of 20 together with a couple of cormorants (*Phalacrocorax c. carbo*) was seen one day on Norman Rock. Most showed the whitish underparts of the immature bird. The 37 eider ducks have already been mentioned. Whether their non-breeding was due to the destruction of nests is not sure. The only other non-breeders were a couple of Sandwich terns, whose nest had probably been destroyed before the party's arrival.

6. Comparison with previous work

The strength of the breeding population on the Isle of May was roughly summarized by Rintoul & Baxter in 1925 (**2**) and there are some interesting comparisons. In 1936 there was no sign of the carrion crow which they record,

nor of the moorhen noted by Elder (**3**), though the former bred until 1929 (L. J. Rintoul in private communication). Other variations are in the starling, recorded as 25 pairs in 1924, and "decreasing" in 1925; in the pied wagtail described as "stationary"[1] (presumably at the figure of 3 or 4 pairs mentioned (**4**)). The eider is difficult to assess, but it appears as if there had been probably some falling off from the figure of 83 pairs in 1925. Meadow and rock pipits are said to have been "decreasing", the only known figures being 3 pairs of the former in 1924 and 31 pairs of the latter in the same year (L. J. Rintoul, private communication).

On the other hand many species have increased: the house sparrow, which had settled at about 2 pairs in 1924, has now risen to 6; while the song thrush, which was then lost, recommenced breeding in 1931 (H. F. D. Elder in private communication) and is now represented by 2 pairs. The blackbird has similarly regained ground, for only one female was seen in 1925 and it did not recommence to breed until 1930 (L. J. Rintoul). The wheatear was confined to 2 pairs in 1925, and in spite of the approximate nature of the estimate given here, shows a clear increase, while the same applies to the shag and the fulmar, both quoted at about 2 pairs.

The increase of the herring gull is quite remarkable; from 58 pairs in 1924, the figure now stands at 455. Unfortunately nothing is known about the intervening years, so that the curve of increase cannot be plotted with accuracy. The lesser black-backed gull is a comparative newcomer, 2 pairs being recorded by Rintoul & Baxter in 1933 (**5**), and it seems probable that their increase will continue.

The only other figure of interest is that for the oyster-catcher, which is said to have risen to 7 pairs by 1921, and to have continued at that until 1925. There may have been slight fluctuations in the intervening years, but evidently the figure is a very steady one, for my census gives exactly the same number of pairs.

7. Acknowledgements

In conclusion the author wishes to express his gratitude to the Commissioners for Northern Lights for permission to stay on the island and for other favours; to the Chief Lighthouse Keeper and other members of the staff for their great help and agreeable company; and to the Midlothian Ornithological Club for the interest and co-operation they displayed, as well as for the use of the Observatory.

C. SUMMARY

A. Twelve house mice (*Mus musculus*) were trapped in buildings and in field walls. Their measurements and parasites are recorded. They belonged to a comparatively large race.

[1] Four pairs bred in 1924 (L. J. Rintoul).

B. A breeding bird census of the Isle of May was carried out in July 1936. The methods are described. The chief care was to produce definition in the figures, with the greatest possible amount of accuracy, to form a concrete basis for comparison with (*a*) the fluctuations due to migrant Passerines, and (*b*) future estimates of the strength of any or all of the breeding birds. The environment is defined in its main features, and the birds are treated not in their systematic order, but in their natural ecological groups. Finally, a brief comparative account of the numbers found by previous workers is given.

REFERENCES

1. **Rintoul, L. J. & Baxter, E. V. (1935).** "Vertebrate fauna of Forth." Edinburgh p. 63.
2. **Rintoul, L. J. & Baxter, E. V. (1925).** Scot. Nat.: 175.
3. **Elder, H. F. D. (1935).** Scot. Nat.: 47.
4. **Rintoul, L. J. & Baxter, E. V. (1918).** Ibis: 264.
5. **Rintoul, L. J. & Baxter, E. V. (1933).** Scot. Nat.: 182.

ERRATA

"A contribution to the ecology of a grassland community on Guadalcanal Island, British Solomon Islands Protectorate.' *J. Animal Ecology*, 1937, Vol. 6, pp. 291–7.

Page 295, line 4. Omit the word flycatcher.

Page 295, line 6. Add nests in *Themeda*.

Page 296. After Hymenoptera delete (18) and substitute (21).

Add, after *Sphex cognatus* Sm. Prey of spider A 2.

Substitute wasp for bee for two species of *Polistes*.

Add: *Crocisa gemminata* Ckll. On leaf tip of *Imperata*.
Polistes variabilis F.
Eumenes latreillei Sauss., var. *petiolaris* Schulz.

Line 7 of text. For temperature read temperate.

REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 26, No. 1, February 1938)

This number of 254 pages contains eleven original papers and four reviews, together with the customary annual report of the activities of the British Ecological Society, together with list of members and statement of accounts.

The original papers include three dealing with different forms of survey work. C. J. W. Pitt-Schenkel describes the important plant communities of a warm temperate rain forest (dominated by camphor-*Ocotea*) at Magamba, West Usambara in the Tanganyika Territory. W. Davies describes the vegetation of grass verges and other excessively trodden habitats in Britain, and N. Mary Martin the epiphytic moss flora of trees in Argyll and the effects on this flora of exposure and of the nature of the tree bark.

A. S. Watt contributes part 3 of his studies in the ecology of Breckland, which deals with the development of *Festuco-Agrostidetum* on infertile sand and with the role of moss-lichen communities in this succession.

Three papers deal with marine or maritime plants and their habitats. Dorothy C. Gibb describes the composition of the algal communities of Castletown Bay, Isle of Man and their relation to tidal range and season, while M. B. Hyde presents data on the effects of temperature and light intensity on the rate of apparent photosynthesis in *Fucus serratus*. V. J. Chapman ("Studies in salt-marsh ecology, I–III") discusses the habitat factors operating on the Norfolk salt marshes, and particularly the effects of tidal range, soil drainage and aeration.

Two papers by W. H. Pearsall on the soil complex in relation to vegetation deal respectively with oxidation-reduction potentials in soils and with characteristic woodland soils. J. F. Hope Simpson contributes a comparative analysis of the flora and soil conditions of a small calcareous area on the Lower Greensand, giving lists of calcifuge and calcicole species. Oliver West discusses the method of determining changes in grassland composition and the statistical treatment of results.

W. H. PEARSALL.

THE ECOLOGICAL METHOD

J. W. Bews (1937). *Life as a Whole.* 347 pp. Longmans, Green and Co. Ltd., 39 Paternoster Row, London, E.C. 4. Price 15*s*.

Life as a Whole supplements Dr Bews's previously published *Human Ecology* and purports to demonstrate, in its discussion of the autecology and synecology of mankind, the ecological method. As yet there has been no serious statement of the ecological position, most writers having left it to be inferred from their accounts of ecological activities. Much, however, has been said and written about the "ecological point of view" or ecology "as a point of view", but there has been little indication of where an enquirer should stand in order to inspect the panorama which, presumably, is offered to him. The ecological *Weltanschauung* is, we may suppose, fairly clear to those initiated into it, since, as Dr Bews remarked in his earlier work, it produces so much enthusiasm. Ecologists must now stand indebted to Dr Bews for the first expanded and, on the whole, clear statement of the meaning of their subject and the source of their enthusiasm. That they may not agree with his interpretation and that he has ignored alternative versions, is beside the point. He has, at least, given a basis for argument.

Ecology, for Dr Bews, is the practical application to nature of General Smuts's philosophy of Holism. The principles of this philosophy are now of general familiarity and there is little need to dwell on them here. "Holism...recognises the tendency of reality everywhere to create wholes, each whole being an integrated structure, which is something different from the sum of its parts." The process of the "creation of wholes" is known to all ecologists. It is expressive of the tendency of systems towards more complete stabilization; a process recognized in the progress of the sere to the climax or of the subsiding into steady rhythm of a predator-prey fluctuation. Ecology recognizes these "wholes" and its appointed task is to analyse them and having done so, to make syntheses in which integrations, formerly hidden, become apparent. Now, if this is the meaning of ecology, various questions arise of which one may be asked. In what way does ecology differ from other biological sciences?

Some difference is clearly implied. It is stated that this holistic (and hence ecological) method provides an alternative to the "merely mechanistic and analytical approach to scientific problems". Yet it is difficult to see the difference between the ecologist who "works by collecting facts, classifying them and arranging them, and fitting them together into constructive syntheses", and another scientist who does precisely the same thing even if he does call his constructive synthesis an hypothesis. In fact, so far as it implies the use of procedures differing from what is usually called the scientific method we must infer that the "ecological viewpoint" is meaningless. Unless, indeed, geneticists and cytologists, embryologists and physiologists, let alone astronomers and psychologists, are, if good scientists, also unwittingly ecologists. And, although this may seem nonsensical, Dr Bews cannot think so—and he is by no means alone in his belief in the magic powers of the ecological arcanum—for he states that the adoption of "the ecological standpoint" is "the beginning of wisdom". This exaltation of their subject may be familiar to many people, it being a feature often present in the writings of American ecologists, but evidently there is confusion of thought behind it.

Ecology should not be confused with the conclusions it draws nor with the organicist or holistic philosophies it uses to form a unifying background to the natural complexities it reveals. It may well be that ecology will provide evidence for the truth of such philosophies, but it should not be identified with them. It should be remembered that other branches of biology also use these methods of thought, and it will be found that their implications have been very thoroughly explored by non-ecological biologists, for example in the writings of Woodger, Needham, von Bertalanffy; and ecologists might well profit by occasional returns to the laboratory science they often affect to despise. The views of Dr Bews and others who exalt the ecological viewpoint as the key to knowledge will be vindicated when other older established sciences acknowledge themselves but offshoots of the super-science of ecology.

Little space is left to remark on the data Dr Bews uses in his discussion of human ecology. The first half of the book is devoted to a discussion of the morphological, physiological and psychological changes occurring during the life of a typical specimen of mankind. The second forms an account, necessarily rather superficial, of human activities. Here, especially, Dr Bews's notions of the scope of ecology have led him away from what might be supposed its legitimate province. We learn that Cézanne had the makings of a good ecologist; though an artist who certainly has some claim to that title, H. G. Wells, is only mentioned as a novelist. There are lengthy catalogues of human notabilities from Thales to A. N. Whitehead, from Palestrina to Schönberg, but no mention of human population changes and the work of the demographers.

It is probably true that ecology tends more than most sciences to encourage a broader outlook, but to pretend that it is the fount of all wisdom is vanity.

JOHN FORD.

THE SURVIVAL OF MAMMALS

(1) **Joseph Grinnell, Joseph S. Dixon & Jean M. Linsdale (1937).** *Fur-bearing mammals of California. Their natural history, systematic status, and relations to man.* 2 vols., 777 pp. and 13 coloured plates. University of California Press, Berkeley, California. Price $15.

(2) **Lee R. Dice & Philip M. Blossom (1937).** *Studies of mammalian ecology in southwestern North America, with special attention to the colors of desert mammals.* 129 pp., 7 text-figures, 8 plates. Carnegie Institute of Washington, Publ. No. 485.

(1) It is elementary to state that wild animals can be successfully conserved or controlled only through long term programmes based on sound knowledge. Despite this, the administrative system in most of the United States and Canadian provinces makes it possible for the personnel of the department in charge of wild life to change with the electoral complexion. For this reason the State or Provincial universities and museums are of immense importance as permanent centres for the accumulation of data and the maintenance of organized research. The two volumes under review are an excellent example of the manner in which this function should be fulfilled. Here is set out that broad basis of fact which should be available in every state or province where wild animals are important assets or liabilities.

As an example of wise legislation the authors cite the policy of the California Fish and Game Commission in 1911–15 when beaver could be taken only under special licence. This was granted (without too much "red tape") for areas where their burrowing and dam-building habits had made them a nuisance or danger. In 1920 beaver ranked tenth in value of the fur bearers of California; but through the present lack of State protection they are in serious danger of extermination. In the period 1920–24 the striped skunk headed the list in aggregate value to trappers. Because skunks are widely distributed and easy to trap they are a source of income to many people to whom the money is the difference between a livelihood and penury. Yet general appreciation of the value to the state of such an animal as the skunk may easily be prevented by outcries against its often imaginary depredations. The true picture of an animal's worth can only be gained from an impartial survey such as these authors present. Those *individuals* should be destroyed that cause economic loss, but for aesthetic, recreational, humane, ecological and economic reasons, wholesale slaughter should not be tolerated.

The treatment of the material is first a description in small type of the systematics of each race or species. This is followed by a variety of natural history observations, distribution, population trends and densities, estimates of economic position, and recommendations. The editing and weighing of the information gathered direct from trappers, sportsmen and others are very carefully done and show the continual importance of this phase of ecological research. The fine coloured illustrations by Major Allan Brooks are another powerful attraction of these volumes. The chapter on "population trends of fur bearers" is a particularly able analysis of the factors responsible for the state's declining fur resources. It is to be hoped that the direction of this trend will be altered through wise use of the information so well presented here.

(2) One of the frequent differences between "natural history" and modern ecology is that in the latter certain natural phenomena are expressed in terms of measurable units. This possibility is usually dependent on advances in technique. In the past few years methods have been developed by Dice and his co-workers of expressing the colours of mammal skins through the use of a tint photometer. Readings are taken principally of the reflected red, green and blue-violet, low readings indicating a dark colour. The technique is now extended to the measurement of the colour of surface soils.

South-western Arizona especially is characterized by well-pronounced life belts, more or less closely correlated with altitude: montane forest, encinal (i.e. characterized by oak and

sycamore associations), arid grassland, desert. The desert soils are pale, those of the montane belt are dark, and soils from the other belts have intermediate tint photometer readings. These differences are due to differences in amount of humus which is determined through the influence of atmospheric humidity on vegetation. 473 individuals of some 20 species were examined and a close correlation was found between pelage colour and life belt.

Much of the country consists of desert, out of which isolated mountains rise sharply. Some of these are composed predominantly of rocks of one colour. The pocket mouse *Perognathus intermedius* is largely confined to these rock hill habitats, and between the colour of the dorsal pelage of its several subspecies and that of the rocks there is a correlation coefficient as high as 0·8. Through the work of F. B. Sumner, the deer mouse *Peromyscus* has become a well-known example of the many species that exhibit geographic colour variations, light- and dark-coloured races often appearing on soils respectively of light and dark colour. The facts of this matching of soil by pelage cannot be explained by the operation of an internal factor alone or by differences in climate or vegetation. Two isolated mountains with different coloured rocks but with apparently identical climate and vegetation may support one a pale-, the other a dark-coloured race of the same species. Natural selection acting through some agency such as predators seems the most logical explanation for the differentiation of these local races. Isolation has no doubt been of importance; but where two races have contiguous distribution, inter-breeding does not result in general obliteration of the sub-specific differences. This seems to indicate the continued operation of the process which has differentiated the sub-species; but there is no reason to believe that the same process will eventually produce distinct species.

The first 73 pages of this paper contain the solid data resulting from the field surveys: description and classification of the biogeography and of the various species and associations. This section naturally requires careful study which might have been aided by incorporation of the plates in the text instead of at the end. The main thesis is well developed and easy to follow, since it is based on sound data adequately presented.

DENNIS CHITTY.

BIRD POPULATIONS

(1) **Margaret Morse Nice (1937).** *Studies in the life history of the song sparrow*, Vol. 1. Trans. Linn. Soc. New York, 4 : 1–247. The Linnaean Society of New York, c/o American Museum of Natural History, 77th St. and Central Park West, New York City. Price $1·50.

(2) **Aretas A. Saunders (1936).** *Ecology of the birds of Quaker Run Valley, Allegany State Park, New York.* New York State Museum Handbook No. 16 (New York State Museum Albany, N.Y.), 68 illustrations, including map. Price 50 cents.

(1) The modern technique of trapping and colour-ringing makes it possible to keep track of individual birds in the field. Anyone who reads this paper will be struck by the number of problems to which this method offers a new approach. The observations recorded are the result of eight years' intensive study of the song sparrow (*Melospiza melodia*) on a 30-acre strip of land near Columbus, Ohio. This land, which at first was waste, was later brought under cultivation. The work of the first year was confined to an intensive study of two pairs, and provided a valuable basis for the more extended observations which at one time covered 75 ringed males. The resulting survey is extremely comprehensive, covering migration, ecological relationships, territory, nesting parasitism by cowbirds, survival rates, age, and population fluctuations. A study of behaviour in more detail is reserved for a second volume.

The points of most general interest arise in connexion with migration and population. There were four categories of song sparrow in the area—resident, summer resident, winter

resident, and passage migrant, and it is to be noted that in a population showing "individual migration" of this type, permanent residents can only be distinguished by the ringing technique. The majority of birds under observation were consistent in migratory behaviour, but of a total of 55 males and 42 females six males and one female changed status, all but one of them becoming migrants after a period of residence. The genealogy of several families was worked out with reference to migration, but the results, while showing that the original idea of a sex-linked control is untenable, are not extensive enough to allow of further genetical analysis. It may be noted that the fact that birds can change their migratory status, does not, as the author suggests, exclude the possibility of an underlying genetical control; the proportion of changes is low.

The spring migrants tended to arrive in two distinct waves, and a close correlation was obtained between the time of arrival of the first wave and the air temperature. This is somewhat at variance with the views of many other authorities, who believe that temperature, particularly at the point of arrival, is of little importance. The suggestion is made that the early wave consists of birds strongly influenced by actual weather, while the main wave birds are largely controlled by "instinct" (more probably by increase of light). The temperature threshold for the arrival of the main wave is considerably lower than that for early birds, which suggests that temperature is not the fundamental factor but may exert a modifying effect on the general behaviour pattern.

The questions of age, mortality, and survival rate, are dealt with in some detail. During the third winter the land was brought under cultivation, and much of the undergrowth cleared, with the result that the population decreased sharply, mortality of adults during the breeding season being particularly high. This is believed to have been due to the increased effect of predators in a more exposed habitat, though evidence on this point is scanty. The general course of events is in accordance with the view that instability of the environment is an important cause of population fluctuation.

This is a stimulating paper with a bearing on several controversial questions. It provides a striking example of the value of continued study of individual birds, and it is to be hoped that other workers will be encouraged by it to undertake similar studies of common species. In conclusion mention must be made of the excellent summaries given at the end of each section.

(2) This paper is an enquiry into the numbers and distribution by habitat of the breeding bird population on an area of 17000 acres, combined with a more intensive study of one species, the ruby-throated humming-bird (*Archilochus colubris*). The areas and limits of the different habitat types were determined by sketch-mapping and traverses, checked where possible by rough triangulation. Sample areas were then laid out in each type of habitat, and the birds of each species within the area counted. Subsequently it was found possible to replace this rather laborious method by a series of travelling censuses, all distances being estimated by pacing, and all birds within fifty double paces on either side of the line being counted.

Counting, wherever possible, was based on singing males, and was carried out early in the morning during the first fortnight of July. Presumably all the actual counting was done in the same year, though this is not made clear. It is to be regretted that no information is given as to the percentage of the total areas actually sampled, as this would be of interest to those engaged in similar work.

A concise description of the plant ecology of each habitat is given. Only 10% of the whole area can be classed as open, and this includes meadows, field pastures, orchards, stream banks and buildings. The distribution of birds in these areas calls for little comment, the numbers and density of species increasing with the increase of trees and shrubs, and reaching a maximum of 15 species and 2·96 pairs to the acre in orchards. In the woodland areas two main forest types, oak-hickory and maple-beech, are distinguished, the latter predominating. Periodic felling and clearing in the maple-beech forest has produced areas of different ages, and hence it was possible to obtain some idea of the succession of bird species as re-afforestation progressed. The young "sprout-forest" is populated mainly by typical pasture-land species, which disappear when the forest canopy closes, being replaced gradually by wood-

land forms. The appearance of the latter can be correlated with such features as the development of humus and undergrowth and the accumulation of dead trees. The total number of breeding birds increases in proportion to the height of the trees.

The observations on the humming-bird include nest sites, nest materials, food competitors, pollination, and numbers. It was found that the basic food was the nectar of the bee-balm (*Monarda didyma*) which may grow either scattered or in clumps. The position of the clumps determined the site of nesting territories. The method of counting was thus to record the total number of clumps and then estimate the population from careful observations in a small area. The patches of bee-balm fluctuate from year to year, producing a corresponding shifting of nests. The males do not usually remain through the nesting season, but when present they occupy territories of their own, as do the nesting females. An instance is recorded of a male and a barren female fighting continually over a single territory.

Although much of the subject matter will appeal only to those who are familiar with American birds, the observations on succession are of some interest. Since they were confined to one year, the picture presented is that of a population at a given moment, and the bulk of the paper is necessarily purely descriptive.

C. H. HARTLEY.

THE NICHE OF THE LITTLE OWL

Alice Hibbert-Ware (1938). *Report on the Little Owl Food Enquiry, organized by the British Trust for Ornithology.* 74 pp. Illustrated by photos. H. F. and G. Witherby, London. Price 3*s*. 6*d*.

This publication is the result of a specific enquiry conducted for a specific purpose, so it is not for the ecologist to complain if figures that he would very much like to have seen are missing. The object of determining the precise qualitative nature of the food of the little owl (*Athene noctua vidalii*), and more generally its quantitative composition, has been most successfully carried out. The wild allegations that have been made about the depredations of this species have been answered in the most effective way.

The section on distribution and numbers is interesting: after its initial introduction into this country between 1894 and 1900 the little owl spread rapidly and became very abundant in places. Now reports indicate that in most districts the population is either stationary or falling off, while there are only two indications of actual increase (in the West Riding and Carmarthen). Censuses give from 2 to 4 pairs in a half-mile radius of favourable country.

The food analysis was made from three sources: 2460 pellets, 76 nest contents and 28 gizzard contents. The tables giving some of these results are not as consistent in form as might be desired, but the general conclusions are quite clear. By far the greatest proportion of the food is insects, this being particularly the case outside the breeding season. The appearance of great numbers of any particular species is immediately reflected in the food: those most commonly taken were crane-flies (*Tipula*), earwigs (*Forficula auricularia*), ground-beetles (*Pterostichus madidus*), dor-beetles (*Geotrupes stercorarius*) and cockchafers (*Melolontha vulgaris*), all but *Geotrupes* notified as pests by the Ministry of Agriculture.

Birds and small mammals were taken in some numbers during the nesting season, starlings (*Sturnus vulgaris*), sparrows (*Passer domesticus*) and Turdidae being the commonest of the former, and house mice (*Mus musculus*), wood mice (*Apodemus*), field voles (*Microtus*), bank voles (*Clethrionomys*) and shrews (*Sorex*) the commonest of the latter.

Apart from these, frogs, lizards, rabbits, rats, various species of small birds, earthworms, woodlice, spiders, millipedes, snails and Lepidopteran eggs were recorded in some numbers.

A special enquiry was conducted during the second year into the food of birds that were breeding near poultry farms or game preserves, which showed that this form of food was negligible. Tests proved that such food would appear in the pellets of captive little owls fed with chicks.

Cognate biological points are dealt with, showing that the species is largely a crepuscular or nocturnal feeder (hence game and poultry would be little affected), that it is primarily a ground feeder, that it does not "store" food, and that it does not kill and leave carcases in order to collect the burying beetles later. This part of the report is mixed up with considerable quotation of opinion, and is not perhaps set out to the best advantage.

The work as a whole however is thorough and authoritative, the plates are to the point, and the pains taken by Miss Hibbert-Ware in the analysis may serve as an example to others.

H. N. SOUTHERN.

SHORT REVIEWS

Cynthia Longfield (1937). *The dragonflies of the British Isles.* 220 pp. and 260 illustrations. F. Warne and Co. Ltd., Bedford Court, Bedford Street, London, W.C. 2 and 381 4th Avenue, New York. Price 7*s.* 6*d.*

This book is a useful addition to the slowly growing list of competent entomological handbooks. It contains a key to the identification of the species of Odonata for field use, information on their collection and preservation, a lucid and interesting account of life histories, general biology, ecology and palaeontology. Descriptions of individual species, imagines and nymphs, are given, together with notes on habits, times of appearance and distribution. There is also a section on the classification of Odonata, in which families and genera are described, chiefly according to wing structure. Finally the book contains a glossary, a pronunciation guide to Greek and Latin names, a list of the times of first appearance of species, a check list of all British species and a complete index. There is an abundance of illustrations, both photographs and drawings. It seems a pity that in the set of drawings of wings, for purposes of comparison, some should be of left and others of right wings. The photographs of imagines and nymphs are admirable.

The key to species is intended, and is only suitable for, field work, being based chiefly on colour differences and therefore inadequate for identification of preserved material. A feature of the book which is not entirely successful is the attempt to provide popular names for species. The distinction between "dragonflies" for the Odonata as a whole and "dragonflies" for the Anisoptera is confusing. The Zygoptera are distinguished by their old name of "damsel flies". The book, though intentionally popular, should prove of great value both to entomologists and ecologists.

JOHN FORD.

Victor E. Shelford (1937). *Animal communities in Temperate America, as illustrated in the Chicago Region: a study in animal ecology.* The Geographic Society of Chicago, Bull. No. 5: 1–368, 315 illustrations. The University of Chicago Press, Illinois. Price $3.

This monograph, originally published in 1913, is reprinted here without substantial change, except for the addition of some later references to the literature on the ecology of the region. All zoological libraries should have it; and many ecologists will be delighted to be able to obtain at the reasonable price copies of a "classical" work which had become rare in book-shops. But more than that: in re-reading it they will be able to recall some of the freshness and sense of space and grandeur that the field work of primary ecological survey can give, and which is so easily lost under the later burdens of indoor sorting, noting, identification and the general deluge of detail—not to mention the close intricacy of experimental studies and the nightmare of literature. Prof. Shelford's original survey was a remarkable feat of industry and organization, as well as being a pioneer research. Its clear presentation is enhanced by the abundance of illustrations, which give reality to the Latin names of animals mentioned. There is, as yet, no parallel survey in Great Britain which comes anywhere near the scope of this comprehensive account of the Chicago country ecosystem.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts are issued free with the *Journal*. They can also be obtained separately in stiff covers, printed on one side of the page to allow them to be cut out for pasting on index cards, by non-subscribers, from the Cambridge University Press, Bentley House, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free, (about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, J. R. Carpenter, D. H. Chitty, C. Elton, F. C. Evans, J. Ford, and B. M. Hobby.

I. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) Marine and brackish

See also **9, 13, 46, 112**

1. Crawford, G. I. (1937). "The fauna of certain estuaries in West England and South Wales, with special reference to the Tanaidacea, Isopoda and Amphipoda." J. Mar. Biol. Ass. U.K. 21: 647–62.

Estuaries of the Plym and Exe, Taw, Camel, Towy, Tamar, Tavy and Lynher were examined and the Crustacean fauna analysed. Notes and literature on brackish-water Crustacea in England, together with a discussion of the English species of *Gammarus*.

2. Anon. (1937). "Excessive marine growth in Shoreham Harbour." Nature, Lond., 140: 966.

Warm water in the Southwick basin of this harbour is apparently the chief cause for extreme growth of a Polychaete worm resembling *Hydroides norvegica*, but possibly new to science.

3. Fisher, N. (1935). "The marine Mollusca of Magilligan. Co. Derry." J. Conch. 20: 168–75.

List of 162 species of shells thrown up on Magilligan strand, with a topographical description of the district.

4. Crawford, G. I. (1937). "Notes on the distribution of burrowing Isopoda and Amphipoda in various soils on the sea bottom near Plymouth." J. Mar. Biol. Ass. U.K. 21: 631–46.

Collections made with a fine-meshed dredge and a D-net. Distributional notes are given on species inhabiting intertidal areas as well as below the low-water mark. Full Appendices of collecting stations, soil types and fauna lists.

5. Raitt, D. S. (1937). "On the occurrence of *Gammarus* in Scottish coastal, brackish and inland waters." Scottish Nat.: 155–61.

A review of the literature concerning the presence of the four species of this Amphipod.

(b) Freshwater

See also **5, 13, 37, 46, 53, 79**

6. Hamilton, D. (1937). "Grebes and other birds at Linlithgow Loch." Scottish Nat.: 129–30.

Observations on grebes in the winter of 1936–7, and some other records.

7. Serle, W. (1937). "The avifauna of Duddingston Loch, Midlothian." Scottish Nat.: 35–45.

A review of the changes in this 19 acre Loch, 1927–36. Ninety-nine birds are discussed and a table concerning the Sept. 1934 to April 1935 weekly abundances of ten species of ducks is given.

8. Eltringham, W. (1937). "A record year on the Crawcrook Pond." Vasculum, 23: 151.

33 waterhens, 20 little grebes and 5 coots were hatched on the two ponds in 1937. The total (58) is the largest in the history of the pond. In a space of 300 by 80 yd. over 200 young terrestrial birds were hatched.

9. Pyefinch, K. A. (1937). "The fresh and brackish waters of Bardsey Island (North Wales): a chemical and faunistic survey." J. Anim. Ecol. 6: 115–37.

32 species found and their distribution discussed in relation to chemical and physical conditions; a special account is given of the ecology of the flatworm *Procerodes ulvae*.

10. Humphries, C. F. & Frost, W. E. (1937). "River Liffey survey. The Chironomid fauna of the submerged mosses." Proc. R. Irish Acad. B, 43: 161–81.

Two stations, one acid and the other alkaline, on moss and liverwort-covered gravel at Ballysmuttan and Straffan, I.F.S., showed that the dominant mosses were *Fontinalis squamosa, F. antipyretica*, and *Eurynchium rusciforme*. 4 subfamilies of Chironomids, including 24 genera and 36 "types" were found. 13 genera and 22 types were common to both stations (at which quantitative samples were taken); 4 new types are described. Orthocladiariae constituted about 95% of the specimens at each station. Seasonal fluctuation in numbers was similar in both stations, maxima occurring in July or August and November or February; minima in May or June and September or October. This study formed part of an investigation of the food ecology of the brown trout (*Salmo trutta*).

11. Rushton, W. (1937). "A further biological study of the River Usk." Publ. Usk Board of Conservators (October): 1–23.

A rather casual survey of some of the animal and plant life of the river and its tributaries, with special reference to the occurrence of trout and other fish, fish foods and sewage effluents.

12. Pentelow, F. T. K. (1935). "Notes on the distribution of the larvae and pupae of *Simulium* spp. in the River Tees and its tributaries." Parasitology, 27: 543–6.

The distribution of five species is described. Suggested factors influencing distribution are geological structure, distribution of water plants and hardness of water. These blood-sucking flies only breed in fast running streams.

(c) Land

See also **42, 43, 45, 75, 106**

13. Tattersall, W. M. (editor) and others (1936). "Glamorgan County History. Vol. 1. Natural History." Wm. Lewis (Printers) Ltd., Cardiff. Price 25*s*.

A survey of the geology, botany, and zoology of the county; with the exception of seaweeds and birds, marine life is omitted. (Reviewed in J. Anim. Ecol. (1937) 6: 386–7.)

14. Watt, H. Boyd (1937). "On the wild goat in Scotland." With supplement: "Habits of wild goats in Scotland", by **F. Fraser Darling**. J. Anim. Ecol. 6: 15–22.

A review of the known history and distribution of goats which have become feral. The supplement contains first-hand field observations in West Ross-shire.

15. Lack, D. & Venables, L. S. V. (1937). "The heathland birds of South Haven Peninsula, Studland Heath, Dorset." J. Anim. Ecol. 6: 62–72.

An ecological survey of the habitats and distribution, including a section on the effects of burning on nesting. Also a discussion on the five most abundant birds. (See also **48**.)

16. Witherby, H. F. & Nicholson, E. M. (1937). "Supplementary notes on the distribution and status of the British willow-tit." British Birds, 31: 104–5.

This species, recorded first in 1900, was formerly confused with the marsh tit. Data obtained on the distribution and relative abundance of these species, up to the present, are recorded. The marsh tit is unknown in Scotland, but the willow tit is known as far north as Ross, Moray and Inverness. Further information is needed.

17. Barnes, H. F. (1937). "Insects and other pests injurious to the production of seed in herbage and forage crops." Herbage Publ. Ser., Imp. Bur. Plant Genetics, Bull. 20: 1–31 and i-iii.

A summary of the available information concerning some of the insect and other pests injurious to the production of seed in grasses and legumes. Although no references have been inserted, all the facts given here have been checked in the light of the most recent research. 127 spp. of insects (89 genera) and 46 spp. of plants are considered in the 3-page index; while the more important pests fill the main text. It is not always clear whether the information applies to the British Isles.

18. Donisthorpe, H. St J. K. (1937). "A preliminary list of the Coleoptera of Windsor Park." Ent. Mon. Mag. 73: 167–76; 237–46; 273–4.

19. Laing, F. (1936). "*Anoncodes melanura* L. as a destructive insect." Ent. Mon. Mag. 72: 15–17.

Notes on the presence of this beetle in London. The larva is a wood borer, often, though not always, in wood placed near water. Further reference in **K. G. Blair**, *ibid.* 72: 17–18; **R. C. Fisher**, *ibid.* 72: 41–2; **J. J. Walker**, *ibid.* 72: 43.

20. Fisher, R. C. (1937). "Studies of the biology of the death-watch beetle, *Xestobium rufovillosum* De G. I. A summary of past work and a brief account of the developmental stages". Ann. Appl. Biol. 24: 600–13.

21. Edwards, T. G. (1937). "Record of Macrolepidoptera found in a London garden." Ent. Rec. 49:101–3.

A surprisingly long list for such a closely built-up area.

22. Barnes, H. F. (1937). "The hollyhock seed moth (*Platyedra malvella* Hübn.), together with notes on the distribution of *Apion radiolus* Kirby and an associated *Clinodiplosis* species." Ann. Appl. Biol. 24: 589–99.

This moth is limited to the S.E. counties of England. The *Apion* and gall midge are generally distributed throughout England, while the latter occurs also in Wales and Ireland. Degrees of infestation by the moth in 1934 and 1935 averaged 65% of the seed heads and ranged up to 97%. An Ichneumonid parasite *Angitia rufipes* was reared.

23. Holborn, J. M. (1937). "Infestation of willows in Suffolk." Entomologist, 70: 211–2.

Hyponomeuta rorella parasitized by the Ichneumonidae *Herpestomus brunnicornis* and *Angitia armillata* and by the Chalcid *Ageniaspis fuscicollis.*

24. Barnes, H. F. (1937). "The Asparagus miner (*Melanagromyza simplex* H. Loew) (Agromyzidae; Diptera)." Ann. Appl. Biol. 24: 574–88.

Includes notes on emergence, mating, oviposition, life cycle and local abundance of this fly during two years. Three parasites are recorded: the Braconid *Dacnusa ?bathyzona*; a Pteromalid *Sphegigaster* sp.; and a Eulophid *Pleurotropis epigonus.*

25. Varley, G. C. (1937). "The life-history of some Trypetid flies, with descriptions of the early stages (Diptera)." Proc. R. Ent. Soc. Lond. A, 12: 109–22.

The Trypetid flies whose life-histories are described in this paper were mostly found during an ecological study of the insect community in the flowerheads of the black knapweed, *Centaurea nigra.*

26. Spooner, G. M. (1937). "Hymenoptera Aculeata from the North-west Highlands." Scottish Nat.: 15–23.

Records for 20 species with notes on geographic distribution; ants not included.

27. Cowley, J. (1937). "Notes on British Odonata in 1936." Entomologist, 70: 221–2.

Emergence dates of dragonflies in various localities.

28. Rawlinson, R. (1937). "The occurrence of the Amphipod *Talitrus dorrieni* Hunt in Co. Galway, Ireland." Ann. Mag. Nat. Hist. 20: 589–92.

This terrestrial species, hitherto known only from Tresco Island, Scilly Isles, has now been found, in a slightly variant form, in Galway. Some notes are given on the pigmentation of Crustacea.

29. Wilson, G. Fox (1937). "The root-knot eelworm, *Heterodera marioni* (Cornu) Goodey, and its relation to plants growing outdoors in the British Isles and in certain European countries." J. Roy. Hort. Soc. 62: 336–46.

In Great Britain and other countries with a temperate climate this nematode (syn. *H. radicicola* Greef) is primarily a pest of glasshouse plants, such as tomatoes, cucumbers and Begonias. In warmer climates it is a very serious pest in outdoor crops, having been recorded from over a thousand species of plants, including weeds that form reservoir hosts. It has been recorded out of doors in the British Isles from 15 wild and cultivated plants, of which an annotated list is given. The life history etc. are also described.

30. Goodey, T. (1937). "On some new hosts of the stem eelworm, *Anguillulina dipsaci.*" J. Helminth. 15: 215–20.

Parsnip (*Pastinaca sativa*) infected with onion strain; *Primula pulverulenta* and *P. polyantha,* source of infection unknown; swine-cress (*Coronopus ruellii*), infected from Narcissi.

31. Johnson, L. R. (1936). "A note on the occurrence of *Anguillulina dipsaci* (Kühn, 1858) on certain weeds, including a new host record." J. Helminth. 14: 233–5.

Cleavers (*Galium Aparine*), a new host record for this eelworm. Observations suggest this weed and chickweed (*Stellaria media*) may be the intermediate hosts carrying over the parasite from infested oats to beans in the next year.

32. Goodey, T. (1937). "Two methods of staining nematodes in plant tissues." J. Helminth. 15: 137–44.

Substitutes for the expensive osmic acid technique.

(*d*) Small islands

See also **65**

33. Morrison-Scott, T. C. S. (1937). "A note on the distribution of the two shrews found in Jersey." J. Anim. Ecol. 6: 284–5.

Evidence based on owl pellet analyses (which disclosed eight kinds of mammal and two birds) that *Sorex araneus fretalis* lives inland and *Crocidura russula* near the shore.

34. Dowdeswell, W. H. (1937). "Further notes on the Lepidoptera of Cara Island." Entomologist, 70: 169–75.

Includes notes on *Xylophasia monoglypha* being eaten by rats, and its population numbers in relation to melanism.

35. Harrison, G. Heslop (1936). "Notes from the Hebrides." Entomologist, 69: 71–2.

Lepidoptera and Coccids from Mull, Barra, Canna, Raasay and Scalpay: on heather, spruce, *Salix* and mosses.

36. Heslop-Harrison, G. (1936). "A contribution to our knowledge of the Psyllidae of the Hebrides." Ent. Mon. Mag. 72: 48–51.

28 species are now recorded from 12 islands, including Skye, Mull, S. Uist, Barra and S. Rona. They are listed, with their host plants and localities.

37. Harrison, G. Heslop (1936). "Coleoptera from the Outer Hebrides, with an account of a new British species, *Deronectes canariensis* Bedel." Ent. Mon. Mag. 72: 52–3.

Beetles from S. Uist and Barra. *D. canariensis* is an aquatic beetle formerly known from the Canaries.

38. Harrison, J. W. Heslop & Peacock, A. D. Edited by (1937). "The natural history of the Island of Raasay and of the Adjacent Isles of South Rona, Scalpay, Longay, and Fladday." Scottish Nat. (for pages see below).

(In this abstract the islands are referred to by their initial letters)

"I. The vertebrates other than birds and fishes." By **J. W. Heslop Harrison.** Pp. 61–3.

Amphibia: *Molge vulgaris* (R, S, SR), *M. palmata* (R), *Bufo vulgaris* (R, S), *Rana temporaria* ("everywhere"). Reptilia: *Lacerta vivipara* (R, S), *Viperus berus* (R, S) in inverse abundance. Mammalia: *Sorex araneus* (R), *Pipistrellus pipistrellus* (R), *Mustela nivalis* (R), *Rattus norvegicus* (R), *Mus musculus* (R), *Oryctolagus cuniculus* (R, S, SR, L, F, and Guillamon I.), *Lepus timidus* (R), *Cervus elaphus* (about a dozen, formerly 600 on R; about 80 on S including colonists from Skye). Also two species of seals and a porpoise. On Longay, rabbits have almost eliminated grass species, leaving strong associations of unattacked plants like *Solidago Virgaurea*. They have also driven out much of the original vegetation on Guillamon I. (Effect of sheep is not commented upon).

"II. The land and freshwater Mollusca." By **G. Heslop Harrison.** Pp. 64–7.

Probably fairly comprehensive collection, from three summers' work: 36 species from R, 20 from S, 12 from SR, three from L, and five from F. Some general habitat notes are given.

"III. Thysanoptera found on Raasay and Scalpay." By **G. D. Morison.** Pp. 67–71.

12 species of thrips. This note includes some biological information about the species on the mainland, mainly relating to life histories.

"IV. Spiders and allied groups." By **J. E. Hull** and **J. W. Heslop Harrison.** Pp. 107–13.

98 species of spiders, 8 Phalangids, and one pseudoscorpion, with a few vague habitat notes. There is a marked southern element in the spider fauna.

"V. The Eriophyidae, or gallmites." By **J. W. Heslop Harrison.** Pp. 135–7.

30 species, partly identified from the galls alone.

"VI. Hymenoptera Symphyta on the Island of Raasay." By **F. Greenshields.** Pp. 138–44.

36 species of sawflies, of which ten had previously been found also on South Rona. Host plants are given. Ichneumonid *Rhyssa persuasoria* parastic on *Sirex* in pine trunks, was also found, on R.

"VII. The variation of the Lepidopterous genus *Triphaena* in Raasay, South Rona, and Scalpay, with special reference to *T. ianthina* Esp." By **J. W. Heslop Harrison.** Pp. 169–72.

Wide gradation was found in varieties thought to be distinct on the mainland.

39. Various Authors (1937). "St Kilda papers." Oxford Univ. Press. (Not on sale.)

A collection of already published papers on the ecology of St Kilda by members of the Oxford and Cambridge student expedition of 1931. (Reviewed in J. Anim. Ecol. (1937) 6: 392.)

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

See also Section 4, for parasites

40. Bracher, R. (1937). "Ecology in town and classroom." 96 pp. J. W. Arrowsmith, Ltd., Bristol. Price 2*s*. 6*d*.

The plant ecology of streets, waste ground, building sites, etc. (Reviewed in J. Anim. Ecol. (1937) 6: 393.)

41. Anon. (1937). "Eleventh Report of the Committee on the nomenclature and records of occurrences of rare birds in the British Isles, and on certain necessary changes in the nomenclature of the B.O.U. list of British birds." Ibis: 396–402.

Additions to the list of British birds, new British races and changes of name and status.

42. Massee, A. M. (1937). "The pests of fruits and hops." 294 pp. Crosby, Lockwood & Son, Ltd., London. Price 15*s*.

Includes lists of insects attacking various fruit trees and shrubs. (Reviewed in J. Anim. Ecol. (1937) 6: 391.)

43. Chrystal, R. N. (1937). "Insects of the British woodlands." 338 pp. Frederick Warne & Co., Ltd., London & New York. Price 7*s*. 6*d*.

An account of the ecology of British forest pests. (Reviewed in J. Anim. Ecol. (1937) 6: 390–1.)

44. Jepson, W. F. (1937). "Observations on the morphology and bionomics of *Serica brunnea*, L., with notes on allied chafer pests. Part I. The morphology of the larva of *Serica brunnea*, L." Bull. Ent. Res. 28: 149–65.

45. Hodson, W. E. H. (1937). "On the synonymy and biology of the strawberry aphis, *Capitophorus fragariae*, Theo. (1912)." Bull. Ent. Res. 28: 409–16.

Reference is made to the proved capacity of Aphides of the genus *Capitophorus* to transmit virus disease among strawberries, and attention is drawn to the confusion existing as to the actual synonymy of the insect principally concerned. The incidence of the aphis in the field, and the biology as observed in field and laboratory are discussed.

46. Crawford, G. I. (1937). "A review of the Amphipod genus *Corophium*, with notes on the British species." J. Mar. Biol. Ass. U.K. 21: 589–630.

A systematic review of this shallow-water, tube-building genus. A complete bibliography accompanies the discussion of each species; notes emphasize distributional, ecological and morphological aspects. Three new species are described, with figures. The review is supplemented by a key to the valid species.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **2, 11, 15, 69, 103, 110, 112, 142**

47. Lack, D. (1937). "The psychological factor in bird distribution." British Birds, 31: 130–6.

Although environment influences distribution, psychological factors are no less important. Birds are guided in their selection of habitat by features perhaps visually prominent but not essential to their existence. The recognition of such features by the investigator is difficult, but examples of psychological reactions which affect choice of nesting sites and song perches and influence feeding habits, etc., indicate their undoubted importance in bird distribution.

48. Venables, L. S. V. (1937). "Bird distribution on Surrey Greensand heaths: the avifaunal-botanical correlation." J. Anim. Ecol. 6: 73–85.

Discussion on heath succession following fire, and factors limiting bird distribution and breeding territories. (See also **15**.)

49. T[emperley], G. W. (1937). "Disabled birds." Vasculum 23: 150.

Comments on the unusual number of disabled birds seen during the summer of 1937.

50. Savage, R. M. (1937). "The ecology of young tadpoles, with special reference to the nutrition of the early larvae of *Rana temporaria temporaria* Linn., *Bufo bufo bufo* Linn., and *Bombina variegata variegata* Linn." Proc. Zool. Soc. Lond. A: 249–60.

The early larvae of these species do not derive noticeable quantities of food material from their own egg-envelopes, yet they seem to develop faster when allowed to remain on the envelopes. Particulate feeding is impossible in these early stages, as the septum closing the mouth is still entire. The gradual disappearance of the envelopes is probably due to bacterial action.

51. Atkins, W. R. G. (1938). "British fisheries, phosphate and the solar radiation constant." Nature, Lond., 141: 77–8.

Since 1923 there has been a decrease in the phosphate content of the water of the English Channel, accompanied by a decrease of plankton abundance and in turn by a shortage of fish. This coastal water is replenished with phosphate only by the influx of large masses of water from the Atlantic, such as occurred in 1921. This was also the year for an exceptionally high solar radiation and the connexion between the two facts is suggested here as a reasonable speculation.

52. Rosenberg, M. (1937). "Algae and trout: a biological aspect of the poor trout season in 1937." Salm. Trout Mag. No. 89: 313–22.

The exceptionally poor trout season of 1937 in the Scottish lochs was correlated with dense surface growths of Algae, hindering the rise of fish and causing them to seek the deeper waters. These Algal growths are dependent upon a large amount of organic matter, such as was presumably supplied by the abnormally high rainfall in January and February, 1937.

53. Garner, J. H., Brown, F. M. & Lovett, M. (1936). "Report upon chemical and biological survey of the River Holme." West Riding of Yorkshire Rivers Board. 44 pp., 21 tables at the end, 3 maps.

A monthly quantitative survey (March 1933 to July 1934) with 13 stations was made on the 12 mile long stream, which has its origin in the Pennine chain. Pollution occurs from six wool-textile mills and exerts effects on the fauna through the changing of ecological conditions. Certain parts of the stream bed showed partial recovery from the cumulative effects of pollution, but no appreciable change in the fauna was found. It is suggested that certain trade effluents exercise a greater influence on the normal biological conditions of a stream than do sewage effluents of apparently similar impurity. "The standards suggested by the Royal Commission on Sewage disposal are not sufficiently stringent to meet the requirements of the particular case investigated, as they are based entirely on limiting amounts of suspended solids without any reference to biological purification.... However it is admitted that application of biological methods of purification to trade effluents would be both difficult and costly." Tables of faunal and chemical data during the 16 monthly collections are presented.

54. Day, W. R. & Peace, T. R. (1937). "Spring frosts." Bull. Forestry Comm. 18: 1–131. H.M. Stationery Office, London. Price 2*s*. 6*d*.

Full account of research on frost incidence, 1927–35, but especially the late frosts of May 1935, which did wide damage. Refers primarily to meteorology, topography and tree damage, but is of general importance for animal ecology. (Reviewed in J. Anim. Ecol. (1937) 6: 391–2.)

55. Tate, P. & Vincent, M. (1936). "The biology of autogenous and anautogenous races of *Culex pipiens* L. (Diptera: Culicidae)." Parasitology, 28: 115–45.

Artificial lighting inhibited hibernation in an anautogenous race. The females attack birds more readily than man. European autogenous races have been maintained in the laboratory without blood meals through 45–49 generations, lasting over 3 years. Stenogamy and autogeny are hereditary characters.

56. Marshall, J. F. & Staley, J. (1935). "Some adult and larval characteristics of a British "autogenous" strain of *Culex pipiens* L." Parasitology, 27: 501–6.

Certain strains of this mosquito are able to mate in confined spaces (stenogamy), to breed throughout the year and to lay fertile eggs without a previous blood meal (autogenous, in distinction from anautogenous strains which do require a meal of blood before fertile eggs are produced). The morphological characters of an autogenous, stenogamic race found at Hayling Island, Hampshire, are described.

57. Ilse, D. (1937). "New observations on responses to colours in egg-laying butterflies." Nature, Lond., 140: 544–5.

Experiments with *Pieris brassicae* showed that egg laying ♀♀ distinctly selected a continuous range from "emerald green" (Ostwald colour No. 22) to "oxide blue" (No. 16), to the neglect of yellow and pure blue. Comparison with colour selection findings for other insects shows a greater degree of discernment of colours in the cabbage white. Selection of purple here appears to be caused by simultaneous colour contrasts.

58. Laing, J. (1937). "Host-finding by insect parasites. 1. Observations on the finding of hosts by *Alysia manducator, Mormoniella vitripennis* and *Trichogramma evanescens.*" J. Anim. Ecol. 6: 298–317.

Alysia and *Mormoniella* are attracted to an environment likely to contain their hosts by qualities of the environment itself, independent of the presence of hosts.... *Trichogramma* is able to perceive its hosts (eggs of *Sitotroga*) by the sense of sight.

59. Jackson, D. J. (1937). "Host-selection in *Pimpla examinator* F. (Hymenoptera)." Proc. R. Ent. Soc. Lond. A, 12: 81–91.

This ichneumon is an internal parasite of Lepidopterous pupae. A long list of recorded hosts is given and the life-history summarized. The development of the larva in hosts of different sizes is discussed. Differences were observed in the reactions of different females to pupae of the same species, some individuals readily ovipositing in naked pupae, others only in pupae within real or artificial cocoons.

60. Hobson, R. P. (1937). "Sheep blow-fly investigations. V. Chemotropic tests carried out in 1936." Ann. Appl. Biol. 24: 627–31.

Account of 42 organic substances used as repellents.

61. Franklin, M. T. (1937). "The survival of free larvae of *Heterodera schachtii* in soil." J. Helminth. 15: 69–74.

This nematode survives many years encysted in soil with no host plant. Experiments show that free living larvae can survive at least 9 months in plant free soil. This must be taken into account in control methods which involve the artificial hatching of cysts.

62. Gibbons, S. G. (1937). "Variations in Copepod development." Nature, Lond., 140: 1064–5.

The suggestion is made that the suppression of stages (from six to five) in the nauplius life of *Eucalanus elongatus* is correlated with a lowering of water temperature.

63. Saunders, J. T. & Ullyott, P. (1937). "Thermo-electric apparatus for limnological research." Int. Rev. Hydrobiol. 34: 572–7.

As a time-saving device, electrical apparatus has obvious advantages for limnology. The resistance method of measuring temperature is cumbersome and difficult to manipulate, and to replace it a thermocouple thermometer with a direct reading scale is described. Hot and cold junctions are connected by copper and constantan wires; the cold junction is maintained at 0° C. by ice in a thermos flask, while the hot junction is in contact with the water to be tested. This apparatus is enclosed in a strong watertight compartment and lowered to the desired depth. A galvanometer introduced into the circuit measures the E.M.F. which bears a linear relationship to the temperature. Thus a direct reading may be had from this apparatus, which is both light and inexpensive. Features of construction and calibration are dealt with thoroughly.

4. PARASITES

See also **23, 24, 38** (VI), **58, 59, 60, 110**

64. Keay, G. (1937). "The ecology of the harvest mite (*Trombicula autumnalis*) in the British Isles." J. Anim. Ecol. 6: 23–35.

Distribution in Britain, hosts, records of Trombiculae on man, and the human diseases carried are discussed. *Trombicula autumnalis* can over-winter on rabbits and bank voles.

65. Thompson, G. B. (1937). "On some parasites obtained from birds on Skokholm Island." British Birds, 30: 317–8.

Ecto-parasites of gannet, Manx shearwater and meadow pipit collected from birds trapped for ringing.

66. Thompson, G. B. (1937). "A list of the Denny collection of Mallophaga in the British Museum (Natural History) and of their hosts." Ann. Mag. Nat. Hist. 19: 74–81.

The material described in Denny's "Monographia Anaplurorum Britanniae", 1842. A list of 117 species, with their type hosts and other hosts recorded by Denny.

67. Gimingham, C. T. (1937). "*Crataerina pallida* Latr., a parasite of the swift (Diptera)." Proc. R. Ent. Soc. Lond. A, 12: 135.

More than twenty specimens of the Hippoboscid fly, *Crataerina pallida* Latr., were taken on a swift that fell to the ground in an exhausted condition at Harpenden in June, 1934. This large number of parasites infesting a single bird would seem to be unusual and the loss of blood due to their feeding may have led to its fall.

68. Thompson, G. B. (1937). "The parasites of British birds and mammals. XVI. Records of Ixodoidea (Ticks)." Ent. Mon. Mag. 73: 160–2.

Ixodes ricinus on red grouse, rabbit, mountain hare, common lizard, dog, cow and lambs. *I. hexagonus* on blue tit and wren. *I. canisuga* on house sparrow and *I. putus* on gannet.

69. MacLeod, J. (1935). "*Ixodes ricinus* in relation to its physical environment. III. Climate and reproduction." Parasitology, 27: 489–500.

Humidity and temperature in relation to oviposition and development. Humidity is the more important, save at extreme temperatures. The lower limit of humidity for development is about 80% R.H. The limits of temperature and humidity are not the same for development and oviposition, the latter being the lower.

70. Radford, C. D. (1936). "Notes on the mites of the genus *Myobia*. Part III." Northw. Nat. 11: 34–9.

Descriptive notes and drawings of 4 species. A new muskrat mite is named *Myobia zibethicalis*.

71. Radford, C. D. (1936). "Notes on mites of the genus *Myobia*. Part IV." Northw. Nat. 11: 144–51.

Includes drawings of 4 species, with descriptive notes. A new species, *Myobia blairi* is announced. An Appendix lists the species of *Myobia* and their hosts.

72. Thompson, G. B. (1937). "The parasites of British birds and mammals. XVII. A bibliography of the previous records of Nycteribiidae, together with additional records and notes." Ent. Mon. Mag. 73: 274–8.

73. Warwick, T. (1937). "The occurrence of disease among muskrats (*Ondatra zibethica*) in Great Britain during 1934." J. Anim. Ecol. 6: 112–4.

Cases of lung disease and tubercular spleen are cited as being in part responsible for the 1934 decrease in muskrat numbers.

74. MacLeod, J. (1937). "The species of Diptera concerned in cutaneous myiasis of sheep in Britain." Proc. R. Ent. Soc. Lond. A, 12: 127–33.

Until recently it had generally been accepted that "strike" of sheep was due, so far as Britain is concerned, to only one species of fly, *Lucilia sericata*. This finding is challenged: three other species, *L. ceasar*, *Calliphora erythrocephala*, and *Phormia terrae-novae*, were found to occur in Scotland (27 out of 68 cases). Evidence supports the contention that *L. ceasar* and *P. terrae-novae* are primary striking flies, and *C. erythrocephala* a true secondary striking fly.

75. Haddow, A. J. & Thompson, R. C. Muirhead (1937). "Sheep myiasis in south-west Scotland, with special reference to the species involved." Parasitology, 29: 96–116.

Dipterous larvae from cases of myiasis in Ayrshire, Arran, and Argyllshire were bred out and showed that six spp. in addition to the usual *Lucilia sericata* were responsible for secondary myiasis; of these, four are new records for which records are given. The species of blowflies studied were found to hibernate as prepupae, pupation taking place in April or May. The "fly season" lasted approximately from May–September, reaching its maximum in July–August. The flies were found most abundantly in low-lying, sheltered ground, especially where much bracken was present.

76. Fenwick, D. W. (1937). "A census of intestinal parasites of lambs in South Wales." J. Helminth. 15: 169–76.

Tables are given showing the incidence of infection with parasites in different sections of the gut, and the seasonal changes in parasite population density, in lambs under one year old. Of nine worms recorded, four are confined to particular regions of the gut, the remaining five showing greater plasticity. In addition to chemical and physical factors within the gut, external conditions, by their effect on the infective stage, would appear to control the position taken up by the mature parasite.

77. Clapham, P. A. (1936). "Further observations on the occurrence and incidence of helminths in British partridges." J. Helminth. 14: 61–8.

Two cestodes and one trematode are newly recorded from *Perdix perdix*. Incidence of helminth disease in 1935 was low, owing to dry weather. Death from strongylosis is most frequent between October and December and again in April and May. It is suggested that conditions are most favourable in spring and autumn for infection, i.e. damp and warm, whereas in summer drought is a limiting factor and in winter, cold. Factors influencing cestode infestation in partridge and grouse are also discussed.

78. Clapham, P. A. (1937). "On some lesions associated with helminths in birds of economic importance." J. Helminth. 15: 49–52.

Recent opinion tends to discount the danger of helminth infestation. This paper describes pathological conditions in various gallinaceous birds which were undoubtedly due to helminths.

79. Rushton, W. (1937). "Blindness in freshwater fish." Nature, Lond., 140: 1014.

Blindness in a number of yearling rainbow trout was due to the presence of larval forms of the trematode *Diplostomum volvens* Nord. in the lens. This is apparently a new record for Britain. The life history of the parasite is given briefly and shows the alternate host to be a water bird, usually a gull. A later note (1938, Nature, 141: 289) records the same condition in rainbow trout and roach. The disease occurs in Europe, where the parasite is known to have a further intermediate stage in Molluscs.

80. Morris, K. R. S., Cameron, E. & Jepson, W. F. (1937). "The insect parasites of the spruce sawfly (*Diprion polytomum*, Htg.) in Europe." Bull. Ent. Res. 28: 341–93.

A severe outbreak of the spruce sawfly (*Diprion polytomum*) in Eastern Canada led to a request to Farnham House Laboratory to investigate, and if possible collect and export, the parasites of this insect in its native home in Europe. Work started in 1932 and it was found that *D. polytomum* was a comparatively rare insect in Europe, though widely distributed. It is heavily parasitized, 31 species of Hymenopterous and Dipterous parasites having been found up to the present. Nearly 28,000,000 parasitized cocoons and eggs of this and other species of *Diprion* have been collected and despatched from Europe, and work is still continuing. Previous to the present work only 13 species of parasites, a list of which is given, were recorded from this host. Of the 31 species now known, 15 are primary, five can be primary or secondary, and nine secondary only; in two cases the status is not known. Descriptions of all the species are given and in the case of the obligatory and facul-

tative primaries, the biology and immature stages are also described and notes added on their suitability for introduction into Canada. Keys are given to the adult parasites and to the larval stages of the primary and facultative primary parasites. Some practical notes also, including methods of accelerating the emergence of parasites in winter and methods of preparing parasite larvae for examination and identification.

81. Morley, C. (1936). "Notes on Braconidae. XV. Microgasterinae." Entomologist, 69: 39–42, 64–7, 90–4, 115–9, 140–2.

Keys to species, with some notes on hosts and distribution of these parasitic Hymenoptera.

82. Salt, G. (1936). "Miscellaneous records of parasitism. I." Ent. Mon. Mag. 72: 9–12.

Hymenopterous parasites of *Syrphus balteatus* and *S. auricollis* (Diptera) and of *Cephus pygmaeus*, the wheat stem sawfly, with information on the incidence of parasitism.

83. Mansbridge, W. (1937). "Fungus attacking larvae and pupae of Lepidoptera." Entomologist, 70: 187.

Issaria farinosa.

84. Patten, R. (1935). "The life history of *Merocystis kathae* in the Whelk, *Buccinum undatum.*" Parasitology, 27: 399–430.

A Coccidian parasite in the kidney of the whelk. The stages within the primary host are described. The intermediate host is not known, but it is possible that it is a crab or other Crustacean.

85. Jepps, M. W. (1937). "On the Protozoan parasites of *Calanus finmarchicus* in the Clyde Sea Area." Q. J. Micr. Sci. 79: 589–658.

A study of the parasites of this Copepod usually considered to be Protozoa showed the presence of *Blastodinium, Synidinium,* some Gregarines (*indet.*), a new ectoparasitic Ciliate (*Chattonella calani*), *Paradinium, Ellobiopsis, Ichthyosporidium,* and early developmental stages of some Platyhelminths. Sections on *Paradinium* and the effects of plasmodial parasites are included.

5. FOOD AND FOOD-HABITS

See also **10, 11, 12, 33, 34, 108, 116**

86. Nicholson, C. (1937). "Moths eaten by bats." Entomologist, 70: 188.

32 additional species recorded in 1935 and 21 in 1936.

87. Campbell, J. W. (1937). "Birds taking moths." British Birds, 31: 122.

Further notes on this by **R. H. Brown,** *ibid.* 155–6.

88. Thomas, J. F. (1937). "Food of nestling swallows." British Birds, 30: 293–4.

Additions to previous lists. 10 species are recorded, of which eight were Diptera. The Bibionid *Dilophus febrilis* was the most abundantly and most frequently eaten.

89. Middleton, A. D. & Chitty, H. (1937). "The food of adult partridges, *Perdix perdix* and *Alectoris rufa,* in Great Britain." J. Anim. Ecol. 6: 322–36.

Crop contents and seasonal changes in food composition with notes of volume and occurrence. The food follows closely the seasonal cycle of plant life, depending largely on agricultural operations.

90. Dewar, J. M. (1937). "Herring gulls feeding on starfish." Scottish Nat.: 32, 81–2.

Notes on the methods by which *Larus argentatus* swallows *Asterias* and *Solaster*. (See also Oldham, *ibid.* (1937) 49–50.)

91. Carpenter, G. D. H. (1937). "Lizards as enemies of butterflies." Proc. R. Ent. Soc. Lond. A, 12: 157–61.

The point here stressed is the great rarity of marks on the wings of butterflies which can be attributed to the wide mouths of lizards, as compared with the acutely angled beak-marks of birds. Ten examples are mentioned, one of these, captured near Eastbourne, has a rounded mark on the left forewing possibly caused by a green lizard in the south of France or the Channel Isles!

92. Ritchie, A. (1937). "The food and feeding habits of the haddock (*Gadus aeglefinus*) in Scottish waters." Fisheries, Scotland, Sci. Invest., 1937, No. 2: 1–94. (Edinburgh: H.M. Stationery Office. Price 4*s.* 6*d.*)

Of Thompson's three main growth regions, that with the lowest growth rate (central North Sea) is found to be the area of least intense feeding. However between food consumption and growth rate there is often no correlation over small areas. Intensity of feeding is reduced in the spawning season. From Aug.–Dec. Crustacea and sand eels are taken in larger amounts. Seven specific feeding areas are described.

93. Savage, R. (1937). "The food of North Sea herring 1930–34." Ministry Agr. Fish., Fish. Invest. Ser. 2, 15, No. 5: 1–57. (London: H.M. Stationery Office. Price 3*s.*)

In the Shields area *Calanus finmarchicus* was the most important constituent of the food. The date and size of its maximum were closely related to the appearance and size of the herring maximum. The intensity of feeding was greatest in May, with a secondary maximum in August. The latter, though slight, is real, especially when the effect of temperature on rate of digestion is considered. In the northern North Sea *Calanus* composed only about a quarter of the total food, *Oikopleura* being the most abundant food animal. The small size and lateness of appearance of *Calanus* was responsible for poor landings in 1932. However, the 1932 broods were strong, whereas those spawned after the good feeding in 1931 were weak.

94. Fox-Wilson, G. (1937). "*Gryllotalpa gryllotalpa* Linn. in a Hampshire garden." Ent. Mon. Mag. 73: 162.

Cannibalism and other food habits of this mole-cricket.

6. POPULATIONS

See also **7, 8, 14, 22, 34, 51, 53, 73, 77, 78, 93, 115, 135**

95. Chitty, D. (1937). "A ringing technique for small mammals." J. Anim. Ecol. 6: 36–53.

Contains a review of previous studies of small mammal movements by marking methods; describes a new technique of live trapping and ringing, and discusses the interpretation of data thus obtained with especial reference to *Apodemus sylvaticus*, and to the use of marking methods for estimating population densities.

96. Lack, D. (1937). "A review of bird census work and bird population problems. (Adapted from a paper read to section D of the British Association, Blackpool, 1936)." Ibis: 369–95.

A valuable paper giving a comparative list of bird population densities in different types of habitat, using the recommended standard measure of number of adult birds per 100 acres. Human interference with nature appears to cause an increase in the numbers of individuals, though not of species. Methods of census taking, both absolute and relative, are discussed, as well as other problems including habitat variation, food, predators, disease, fecundity, population fluctuations, migration and territory. There is a large bibliography.

97. Vevers, H. G., Fisher, J., Hartley, C. H. & Best, A. T. (1937). "The 1937 census of gannets on Ailsa Craig; with notes on their diurnal activity." J. Anim. Ecol. 6: 362–5.

An increase of 24% on the previous year's census was found, localized in definite regions. Observations on the diurnal activity suggest relation between activity and wind, and the possibility of a rhythm.

98. Robinson, H. W. (1937). "Ringing puffins: good percentage of recoveries on breeding grounds." Scottish Nat.: 24.

Of 120 adults marked in 1937, on an island of the Orkneys, 17 bore rings of previous years. In 1935 individuals ringed as far back as 1928 were recovered. No recoveries were made in the winter quarters.

99. Philipson, W. R. (1937). "Two contrasting seasons at a redwing roost." British Birds, 30: 343–5.

Observations on a Northumberland roost of *Turdus musicus*. Flights to a communal roost were comparable to those made by rooks and starlings. The territory covered by members of this roost in 1934–5 was as great as in 1933–4, although the population density of the roost had considerably decreased.

100. Gladstone, H. S. (1937). "The decrease in blackgame in Dumfriesshire." British Birds, 31: 188–93.

Evidence suggests this may be due to the introduction of pheasants, against which blackgame are unable to compete in the struggle for the same ecological niche. On an area where pheasants were kept down, blackgame continued to flourish.

101. Middleton, A. D. (1937). "The population of partridges (*Perdix perdix*) in Great Britain during 1936." J. Anim. Ecol. 6: 318–21.

Data for nesting, summer sample counts, and shooting records on a number of estates. Nest density reached a maximum in 1936, but an unfavourable summer caused a high mortality among the young birds.

102. Ford, E. (1937). "The nation's sea-fish supply. Being the Buckland lectures for 1936." 112 small pp. Methuen & Co. Ltd., London. Price 3*s*. 6*d*.

Fisheries policy and the need for ecological research in planning conservation of the North Sea fish populations. (Reviewed in J. Anim. Ecol. (1937) 6: 395.)

103. Ministry of Agriculture and Fisheries (1936). "Salmon and freshwater fisheries. Report for the year 1935." 41 pp. (London: H.M. Stationery Office. Price 9*d*.)

This report gives the numbers and weight of salmon and migratory trout caught in 1935 in 27 fishing districts and summarizes the fluctuations in population of these fish since 1905. Furunculosis epizootics are discussed and it is suggested, in the case of the river Coquet, that improvements in fish passes, by permitting a wider distribution of the population, have diminished the intensity of the disease. Pollution and precautions against it are discussed and notice is given of simple methods of oxygen estimation for use by laymen. Relatively heavy and evenly distributed rainfall in 1935 lessened the damage due to sewage disposal. An experiment showed that trout are unable to live in artificially softened water, though the presence of only small quantities of natural hard water (about one thirtieth) keeps the fish healthy.

104. Powell, T. P. P. & Phillips, F. A. (1937). "Wye Board of Conservators: Annual Report, Season 1936." Hereford. 15 pp.

The rod catch of salmon for the season 1936 was, next to that of 1927, the best on record. Owners and lessees returned complete details on all but 146 of 5916 fish taken by rod. The average weight of these fish was 18·4 lb., the best represented group (66 %) being that from 15–< 30 lb. (approximately the 5-year-old class). The group 7–< 15 lb. (4 year olds) was 30 % of the rod catch. There was an unprecedented number of fish over 30 lb., but few grilse. Over 26 tons were netted in the estuaries. Furunculosis was again present.

105. Powell, T. P. P. & Phillips, F. A. (1938). "Wye Board of Conservators: Annual Report, Season 1937." Hereford. 15 pp.

In 1935 and 1936 the Wye experienced good fishing and the salmon rod catch was again easily ahead of those in other English and Welsh rivers. The 1937 season, however, was a very poor one not only in the Wye but in salmon waters throughout England and Ireland. The average weight of the fish taken by rod was 19·7 lb. (a record for the Wye) but this was largely because 5-year-old fish composed the bulk of the catch (80 %) as compared with 14 % of 4 year olds. Failure of the 4-year-old run has occurred as follows: 1918 (961 fish taken by rod and net); 1929 (1288 fish); 1930 (912 fish); 1937 (842 fish: less than one-quarter the average for the previous 5 years). This last failure cannot be attributed to bad conditions during the spawning, fry or parr stages. There seemed to be satisfactory numbers of fry, parr and smolts during 1937. Under nine tons were netted in the estuaries. Furunculosis was present for a fourth year.

106. Baweja, K. D. (1937). "The calculation of soil population figures." J. Anim. Ecol. 6: 366–7.

80–90 % of the soil fauna was found to be restricted to the top 9 in. of soil. It is suggested that samples be made of the size of 3 × 4 in. which is 2/1,044,440ths of an acre, so that calculation of individuals per acre may be facilitated.

107. Pickles, W. (1937). "Populations, territories and biomasses of ants at Thornhill, Yorkshire, in 1936." J. Anim. Ecol. 6: 54–61.

Weights and biomasses for 3 spp. A repopulation of the area disturbed in 1935 had taken place and the territories of the foraging species were found to be the same as for the previous year. *Formica fusca* was found to have the greatest weight (0·011 g.) per sq. m.

108. Carey, E. & Diver, C. (1937). "Territory in the yellow field ant, *Acanthomyops flavus*." J. Anim. Ecol. 6: 193–4.

Shows that this ant has a foraging territory and a preference for certain species of plants.

109. Hanson, H. S. (1937). "Notes on the ecology and control of pine beetles in Great Britain." Bull. Ent. Res. 28: 185–236.

Discusses the economic status of pine beetles in Britain, damage, occurrence of outbreaks, factors influencing the population, silvicultural treatment and forest hygiene.

110. Lysaght, A. M. (1937). "An ecological study of a thrips (*Aptinothrips rufus*) and its nematode parasite (*Anguillulina aptini*)." J. Anim. Ecol. 6: 169–92.

Distribution of this thrips in the "1856" plots at Rothamstead; seasonal distribution of thrips and degree of infestation, 1933–5, and the fluctuations in numbers of the host are discussed. The nematode is absent where there is a rank growth of the grass *Holcus lanatus*.

111. H[arrison], J. W. H. (1937). "The small ermine moth once more a nuisance." Vasculum, 23: 108.

After a period of comparative quiescence the small ermine (*Yponomeuta evonymellus*) has completed defoliated the bird cherry throughout the centre and west of Durham, and in Northumberland along the Tyne Valley.

112. Orton, J. H. (1937). "Oyster biology and oyster-culture. Being the Buckland lectures for 1935." 211 small pp. Edward Arnold and Co., Ltd., London. Price 5*s*.

The life history and autecology of *Ostrea edulis*. (Reviewed in J. Anim. Ecol. (1937) 6: 394–5.)

113. Orton, J. H. (1937). "Some interrelations between bivalve spatfalls, hydrography and fisheries." Nature, Lond., 140: 505–6.

A study on the Cark Sands in Morecambe Bay, together with findings of other workers on the Dogger Bank, show a tendency for *Cardium edule* and *Spisula* spatfalls and other organisms to become concentrated and precipitate in greatest numbers out of the plankton in localities where slack and eddy waters occur.

114. Pierce, E. L. (1937). "A plankton collector for fast towing." Nature, Lond., 140: 1014–15.

This inexpensive instrument consists of a diving fin to which is attached the plankton collector with an internal conical silk net. It is designed to collect living plankton quickly over a wide area and has proved practical when towed at a speed of eight knots. A full description is given together with a photograph of the apparatus.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **95**

115. Parsons, B. T. & Middleton, A. D. (1937). "The distribution of the grey squirrel (*Sciurus carolinensis*) in Great Britain in 1937." J. Anim. Ecol. 6: 286–90.

A comparison of the areas of distribution for 1930, 1935 and 1937 shows that the range continues to increase. The results are shown on a grid map.

116. Fraser, F. C. (1937). "Common dolphins in the North Sea." Scottish Nat.: 103–5.

Notes concerning five strandings on the east coast of England and Scotland in February 1937. Measurements of specimens are given. It is suggested that the dolphins followed cuttlefish which invaded the North Sea, and that the stranding of several sperm whale was due to the same reason.

117. Anon. (1937). "The future of the 'British Birds' Ringing Scheme: Transfer to the British Trust for Ornithology." British Birds, 31: 5–6.

This scheme, started in 1909, is steadily growing and responsibility for it has been undertaken by the British Trust for Ornithology, with headquarters at the British Museum. Enquiries to "Bird Ringing Committee, British Museum (Natural History), London, S.W. 7."

118. Witherby, H. F. (1937). "British Birds Marking Scheme. Progress for 1936." British Birds, 30: 337–42.

Over half a million birds ringed since 1909. Gives the numbers of 107 species ringed, with percentage of recoveries. Lists of persons participating.

119. Anon. (1937). "Recovery of marked birds." British Birds, 30: 254–8, 307–16.

120. Leach, E. P. (1937). "Recovery of marked birds." British Birds, 31: 112–19, 139–43.

Large lists giving date and place of ringing and recovery.

121. Witherby, H. F. & Leach, E. P. (1937). "Movements of ringed birds from abroad to the British Isles and from the British Isles abroad. Addenda V." British Birds, 31: 14–24, 42–53.

Additions, with notes, to the abundant records already published. Revised migration maps are given for heron, teal, wigeon, Manx shearwater and common and black-headed gulls.

122. Midlothian Ornithological Club (1937). "Isle of May Bird Observatory. Autumn Report, 1936." Scottish Nat.: 51–5.

A report on the general migration, ringing (300 adults of 42 spp.), weather conditions, with special notes on the yellow-breasted bunting, the Siberian lesser whitethroat and the northern willow warbler.

123. Midlothian Ornithological Club (1937). "Isle of May Bird Observatory. Spring report, 1937." Scottish Nat.: 126–8.

Report on general migration and weather conditions, 27 Mar.–29 May, and a note on the 449 adult and 13 young birds ringed (8 spp.).

124. Boyd, A. W. & Thompson, A. Landsborough (1937). "Recoveries of marked swallows within the British Isles." British Birds, 30: 278–87.

Young swallows, after fledging and before true migration sets in, disperse in all directions, though not to great distances. Yearling swallows seldom return to the exact spot where they hatched, but commonly to the same neighbourhood. Adult swallows generally return to the same place, often to the same nest as in the previous year.

125. Thomas, J. F. (1937). "Results of ringing and trapping swallows in Carmarthenshire." British Birds, 30: 294.

One male, ringed as an adult in 1931, returned in 1936 to nest within 20 yd. of its original site.

126. Robinson, H. W. (1937). "Recoveries of gannets from the Bass Rock." Scottish Nat.: 133–4.

Localities of 20 recoveries of birds banded since 1926.

127. Blockey, R. (1936). "Experiments with storks during 1936." Bird Notes and News, 17: 57–9, 91.

Attempt to rear storks from East Prussian eggs in a heronry in North Kent failed because the eggs were addled. Young storks sent from the Vogelwaree in Rossitten to the Haslemere Educational Museum lived successfully in Kent from June to August. By early November all had left for Africa *via* Isle of Wight or Land's End; two were killed passing through Normandy, indicating that eastern birds reared and released in the west took western migration route.

128. Anon. (1937). "Large immigration of waxwings in Scotland." British Birds, 31: 86–8.

Occurred in 1937 in February and March, instead, as is more usual, of October and November. Apparently the largest immigration since 1921–2, taking place mainly across S. Scotland from E. to W. as far north as Loch Ness. Notes on food habits.

129. Baxter, E. V. & Rintoul, L. J. (1937). "The immigration of waxwings in spring 1937." Scottish Nat.: 93–101.

An extraordinarily large migration into Scotland in Feb. and Mar. 1937 (which is late for this species); the birds spread rapidly about the country. Notes are on food and habits.

130. W[itherby], H. F. (1937). "The January–February influx of grebes and divers." British Birds, 30: 370–4.

Summary of replies relating to *Podiceps griseigena, nigricollis* and *auritus* and *Colymbus stellatus* and *arcticus*. The principal date of arrival in 1937 was January 31st, some birds remaining until April. This influx is from E. to W. and in 1937 most inland waters had one or two grebes. Tables are given of times and places of arrival and lengths of stay.

131. Temperley, G. W. (1937). "The 'summering' of a brambling near Newcastle." Vasculum, 23: 121.

On 18 September 1936 a brambling came to a bird-table and continued to visit the garden until 17 April 1937. It was seen again at intervals during the summer until the end of September. Normally this species migrates to the north in March or early April.

132. Wood, H. (1937). "Movements of herring in the northern North Sea." Fisheries, Scotland, Sci. Invest. 1937, No. 3: 1–49. (Edinburgh: H.M. Stationery Office. Price 2*s*. 6*d*.)

The author showed previously that in a mixed sample, races and communities of varied origin can be distinguished. If scales are correctly interpreted movements may be traced since the broods are thus naturally "tagged". The herring stocks, mixed together in the northern North Sea (NNS) for feeding during spring and early summer, split up in July:

Group	Spring and early summer	Latter half July	Mid-Sept. on
NNS adult autumn spawners	NNS then W. to N. and E. Shetland	S. to spawn off N.E. Scottish coast (1)	Leave coast. Some E. to Fladen ground (2)
NNS adult spring spawners	As above; greatest density further N. in Apr.–May	Seawards (4)	
SNS adult autumn spawners	Shetland and N.E. Scotland	Fladen ground (4)	S. to spawn (3)

(1) Joined by NNS spawners maturing for first time. These come from the opposite direction: E. coast estuaries and shallower waters of middle North Sea, their habitat during adolescence.

(2) Movements correspond with annual circular movement of water.

(3) Departure causes abrupt change in age composition.

(4) If these groups are numerous in spring and early summer the later catches on the Scottish grounds will be reduced, especially if the other group is small. This happened in 1930 when good landings up to 10 July were followed by some of the poorest for many years.

133. Menzies, W. J. M. (1937). "The movements of salmon marked in the sea. 1. The North-west coast of Scotland in 1936." Fisheries, Scotland, Salmon Fish., 1937, No. 1: 1–17. (Edinburgh: H.M. Stationery Office. Price 2*s*.)

Bag nets were used. Catches were best with an onshore wind and low water in the rivers. Four types of tags were tried; the best resembled a cattle ear tag. Movement in the Moray Firth is mainly of a restricted circulatory character. Short erratic journeys were made by restless fish waiting to ascend the Thurso River. 12 miles south of Cape Wrath the greatest number of salmon caught were proved by scale examination to be of very mixed origin; few were native to the local rivers. After release the fish scattered widely on their spawning migration to the rivers in which they were hatched. One quarter went south (as far as Mull, 150 miles); the rest went east (as far as Norway, 400 miles) or east and south (as far as Whitby, 410 miles). It is probable that up to Cape Wrath a common route had been followed from a feeding ground to the N. or N.W. Rates of travel were up to 33 miles per day.

134. Menzies, W. J. M. (1938). "The movements of salmon marked in the sea. 2. The West coast of Sutherland in 1937." Fisheries, Scotland, Salmon Fish., 1938, No. 1: 1–9. (Edinburgh: H.M. Stationery Office. Price 1*s*.)

448 salmon were caught, tagged and released 30 miles south of Cape Wrath. 13% were recaptured, ⅝ on the north or east coasts, ⅜ on the west. Recaptures were in rivers in which (as proved by scale peculiarities) the fish had been hatched. This confirms previous findings that the N.W. tip of Scotland is visited by salmon on a definite spawning migration route and that dispersion from here is not at random.

135. Nall, G. H. (1937). "Sea-trout of the River Conon." Fisheries, Scotland, Salmon Fish., 1937, No. 4: 1–31. (Edinburgh: H.M. Stationery Office. Price 2*s*. 6*d*.)

Scale reading was complicated by (1) the descent of some fish to brackish water for the last year or two of parr life, where open growth on the scales was made similar to that made by whitling in summer; (2) the occasional absence of a normal winter check due to good feeding; (3) occurrence of false checks due to irregular spring and summer feeding and (4) differences in abundance of food located in first two years after migration resulting in different scale growth. However, standards of average growth were made and interpretations checked by recaptures of marked specimens. Most (68%) migrate after three years of parr life (extremes two and five years) and most (52%) spawn in the second winter after migration (only 3% as whitling).

136. Stephen, A. C. (1937). "Recent invasion of the squid, *Todarodes sagittatus* (Lam.) on the east coast of Scotland." Scottish Nat.: 77–80.

A large number of strandings on beaches in Feb. 1937. There had been no storm. Squid were also abundant in the waters to the north of Scotland in 1930–1.

137. Grant, K. J. (1937). "An historical study of the migrations of *Celerio lineata lineata* Fab. and *Celerio lineata livornica* Esp. (Lepidoptera)." Trans. R. Ent. Soc. Lond., 86: 345–57.

The distribution and outbreaks of the sub-species *Celerio lineata lineata* in America, and *Celerio lineata livornica* in the Old World as far as they are known are described. It is suggested that both sub-species originate in semi-desert areas, and this idea is supported in the case of the American sub-species by showing that a correlation exists between outbreaks of the moths and a certain sequence of desert rainfall. No correlation is found between European outbreaks and the rainfall of those North African meteorological stations for which records are available, but this may be due to the paucity of suitable figures. A full account is given of the occurrence of *C. l. livornica* in Great Britain, and the main European outbreaks are listed. A correlation is given to show that years both of unusual abundance and of absence tend to occur simultaneously in Europe and America, and that the cause of outbreaks must therefore be sought in some factor common to the two continents. There seems to be some correlation between outbreaks and the sunspot cycle, but the figures are barely significant. The outbreaks tend to occur away from the sunspot minima.

138. Grant, K. J. (1936). "The collection and analysis of records of migrating insects, British Isles, 1931–5." Entomologist, 69: 125–31.

A discussion of the type of data required from observers; especially numerical estimates of abundance. Counts of indigenous species such as the small tortoiseshell are now being used as a control for comparison with counts of migratory forms.

139. Dannreuther, T. (1937). "Insect migration in May, 1937." Entomologist, 70: 165–6.

Pieris brassicae and *P. rapae* coming inland in large numbers along the north coast of Norfolk and in East Yorkshire from the North Sea against the wind. Also *Vanessa cardui* moving north from the South of England.

140. Dannreuther, T. (1937). "Migration records, 1937." Entomologist, 70: 176–80.

Records of insect movement during 1937. Further references in *id. et ibid.* 200–2; 228–31; 250–4.

141. Welti, A. (1937). "A collection of Lepidoptera taken between the Tower of London and the Monument, 1925–37." Proc. R. Ent. Soc. Lond. A, 12: 139.

Includes 7 migrants, 11 residents and 10 occasional species.

142. Beauchamp, R. S. A. (1937). "Rate of movement and rheotaxis in *Planaria alpina*." J. Exp. Biol. 16: 104–16.

Continues previous studies of *Planaria*. Feeding increases rate of movement for a period of about ten days. Sexually mature individuals respond positively to a weak current, and move at a faster and more irregular rate than do immature individuals. Negative rheotaxis is caused by strong stimuli or combined weak stimuli. Above 12° C. *P. alpina* responds positively to weak currents—a fact which explains the distribution of this species.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT WRAY CASTLE, WINDERMERE, 28 AUGUST—1 SEPTEMBER 1937

By the kind invitation of the Council of the Fresh-water Biological Association and of the Director of the Station, the Society was able to hold its Summer Excursion at Wray Castle, Windermere. The organization of the meeting was kindly undertaken by the President, Dr Pearsall. About twenty-five members were present: some were accommodated in the Castle and some in Ambleside.

28 *August*. After dinner in the evening there was an informal meeting in the library of Wray Castle. Dr Pearsall gave an account of the general ecology of the area. He pointed out that the rocks are of three main types, the Borrowdale slates which are very hard and give steep acute hills and shallow soil, the Bannisdale slates which are softer and which give lower hills of rounder outline, and a deeper soil, and in the north, the similar Skiddaw slates. There is much superficial drift, and some outcrop of limestone to the south of Windermere. A series of lakes of glacial origin vary according to whether they lie in the softer or the harder rocks. For example, Windermere, which is in the softer rock, shows more silting and a richer vegetation. The high rainfall causes soil leaching which is marked on the deep soils, and has pronounced effects on the vegetation, although it is offset on steeper slopes by the effects of weathering and downwash.

Dr Pearsall pointed out that the area round Windermere has the highest percentage of natural woodland in Britain, consisting mostly of *Quercetum sessiliflorae* in a nearly natural condition. Man has exploited the woods until about eighty years ago for charcoal for iron smelting, producing coppice with standards, containing abundant hazel, birch and ash. Later there was bobbin and gunpowder manufacture. The exploited woods are very mixed, but the native woods have only occasional holly and birch under the oaks. There has also been marked deforestation from 1800 ft. downwards, by sheep grazing on the hillsides, and it was pointed out that this may have begun in prehistoric times, because all Bronze Age remains occur at 1000 ft. or more, save on the exposed western faces where they go down to 500 ft. The grazing is mostly *Agrostido-festucetum*, with *Nardus* where the drainage is locally poor.

The Director of the Station, Dr Worthington, gave an introduction to the work going on in the laboratory, indicating how the production cycles in Windermere were being investigated from many different angles. He briefly indicated the chemical measurements made by Dr Mortimer on the dissolved and suspended substances in the Lake, their seasonal variation and the recent detailed bathymetric survey of the lake by echo-sounding. He mentioned the work of plankton collection and algal culture, carried out by Dr Rosenberg, and the work of Dr Misra in relating rooted vegetation to the nature of bottom deposits. He showed that Misra's conclusion for plants had been extended by Mr Macan to water bugs, different species of which are associated with successive stages in the evolution of the lake-bottom deposits. Lastly he mentioned the work of Mr Allen on studies of the food and growth of fish, particularly of the perch in Windermere.

29 *August*. During the day the party had the opportunity of examining a long series of exhibits showing the work of the laboratory, and of discussing these with the staff. By duplicating the trip, it was made possible for all members of the party to take part in an excursion on the lake in the Station launch.

Lake Excursion

Dr Pearsall and Dr Worthington gave a demonstration of the method of measurement of light penetration into the lake water by means of a Bernheim photoelectric cell lowered on a boom away from the boat. They demonstrated the typical logarithmic fall of light intensity with depth below the surface, and it was explained how light penetration is correlated with density of phytoplankton. It was shown that in a sequence of dry summers the reserves of nutrients in the lake are depleted and light penetration is great, but that rainy seasons, or sewage effluents, cause high phosphates and high nitrogen, with high phytoplankton density and less penetration. It was said also that the depth of rooted submerged Angiosperms depends directly on the light penetration.

The standard method of making a plankton haul was then demonstrated, and specimens were taken back for examination in the laboratory.

Dr Pearsall explained the factors which controlled the distribution of littoral phanerogams. Places with no silt had no plants, with young silt, abundant plants, and with an old, highly evolved, very organic bottom, again no plants. These features were demonstrated in Pullwyke Bay, which shows both a time succession and a zonation. The zonation showed *Phragmites* on the gravel shore, then a belt of *Carex inflata* and then *Scirpus lacustris* or *Equisetum limosum* on organic mud. The more inorganic silts showed *Potomogeton alpinus, Sparganium minimum* and *Elodea* with reed swamp of *Phalaris* and *Phragmites*. The more organic soils carried *Lobelia*, and in the reed swamp, *Equisetum limosum*.

30 *August*. The party visited Roudsea Wood and the adjacent peat moss. The moss is a typical example of a raised bog which has been severely drained and burned. The sphagnum surface is quite dead, but it retains the typical pool and hummock topography. *Myrica, Calluna* and *Erica tetralix* are now dominant with *Scirpus caespitosus* and *Eriophorum vaginatum* abundant, birch seedlings are scattered very abundantly over the bog surface, and the sloping margin of the bog next to the wood is covered with subspontaneous pine-birch wood. *Pinus* and *Betula pubescens* are dominant but make an open stand, and *Sorbus aucuparia* is frequent. The shrub layer is a continuous sheet of very tall *Vaccinium myrtillus. Myrica Ilex,* and *Dryopteris dilatata* are occasional. These pine woods are on the edges of all the mosses, and Pearsall regards them as the relics of native woods; they grow on very highly oxidized and very acid peat of pH 2·8–3·2. *Pteridium* is local on disturbed and less acid soil of pH more than four, often with *Molinia, Hypnum cupressiforme* and *H. schreberi*. In residual wet places on the bog surface the following mosses were recognized, *Sphagnum papillosum, S. plumulosum, S. tenellum, Campylorus flexosus, Dicranella cerviculata.*

Roudsea Wood itself showed a remarkably complex and interesting vegetation related to a striking alternation of limestone outcrops through deeper calcareous clay becoming locally more or less acid. On the clays the woods were of oak-ash type with oak standards and ash copice. *Betula, Alnus, Quercus robur,* and sycamore were present with *Rubus saxatilis, Paris quadrifolia, Melica uniflora, Convallaria majalis.* The deeper soils carry *Brachypodium sylvaticum* and *Mercuralis perennis.* The sharp limestone outcrops were dominated by *Taxus*, but also carried abundant *Alnus, Corylus, Fraxinus, Euonymus, Tilia cordata,* and *Sorbus aucuparia*, with mosses such as *Hypum molluscum* and *Neckera*, and *Convallaria* in the shallow soils.

Where the wood was traversed by a deep valley, an old arm of the sea, there was a wide deposit of alkaline peat maintained by calcareous drainage water. It showed a sequence from *Phragmitetum* through a tussock swamp of *Carex paniculata* to fen wood dominated by *Alnus* and *Frangula alnus*. In many places both the reed swamp and fen wood had been cut, giving the very characteristic fenland patchwork, with all the typical fenland species. On the drained and cut slopes of the valley, the fen peat had become acid, and was covered with

Molinia with *Deschampsia flexuosa* and *Galium saxatile*, or with tall *Pteridium*: *Alnus* and *Betula* were colonizing it rapidly.

On the far side of the valley was fairly primitive oak wood on slate, which had undergone some felling but no coppicing. There were no trees but oak, but there were occasional shrubs of *Ilex*, *Betula*, *Sorbus aucuparia*, and *Tilia cordata*. The shallower soils carried *Rubus*, *Deschampsia flexuosa*, *Galium saxatile*, *Luzula pilosa* and *Teucrium scorodonia*. On the deeper soils there was *Pteridium* with some *Scilla* and *Holcus*, and on the rocky outcrops *Vaccinium myrtillus* with characteristic mosses such as *Mnium hornum*, *Hypnum cupressiforme*, *Dicranum majus* and *Hylocomium loreum*. There were conspicuously more mosses and ferns on the north- and south-facing slopes.

From the wood the party made its way to the shore of the estuary which was bordered by fragments of sandy salt marshes. Locally these marshes gave indications of a transition through *Phragmitetum* into fresh-water fen. After tea the party visited a strip of woodland on thin dry peat about nine inches thick overlying estuarine silt. Here *Betula pubescens* was dominant, with *Acer pseudoplatanus* frequent and *Taxus* rare. On the floor *Dryopteris dilatata* and *Scilla* were abundant, and it was suggested that the fern was the chief peat former.

31 *August*. The zoologists of the party visited Stickle Tarn, a series of peat pools at altitudes from 500 to 2000 ft., and examined the transition from lowland to alpine fauna.

The botanical party was taken to Tarn Howes, on the margin of which they examined a small drainage bog containing a mixture of oligotrophic and eutrophic species. The lake, with water of low hardness, has a Desmid plankton and contains *Litorella*, *Lobelia*, *Elodea*, *Potomogeton natans*, and *Myriophyllum spicatum*. The party then followed the outflow stream from the lake down to the Ambleside-Coniston road, examining on the way the bryophytes of the stream bed, and the fragments of primitive woodland on the valley slopes. Submerged in the stream were *Fontinalis antipyretica*, *Eurhynchium rusciforme*, *Alicularia scalaris*, and *Scapania*. In the splash zone were *Porotrichum alopecurum*, *Brachythecium rivulure*. Abundant on rock slopes by the beck were *Hymenophyllum unilaterale*, *Plagiothecium undulatum*, *Dicranum majus*, *Hylocomium loreum*, on sloping *damp* rock surfaces were *Campylopus atrovirens* and *Rhacomitrium protensum*, and on rock surfaces with acid drainage water *Blechnum*, *Diplophyllum albicans* and *Sphagnum* (?) *quinquefarium*.

The fragments of primitive wood had a very open stand of *Quercus sessiliflora* with marginal *Betula alba*, and a small amount of *Sorbus aucuparia* and no shrubs, or sparse hazel or holly. There were abundant seedlings of *Betula*, *Sorbus*, *Fraxinus* and *Quercus*, but few seedlings were surviving. The ground was completely carpeted with vegetation, mostly mosses. The Phanerogams included *Vaccinium*, *Galium saxatile*, *Potentilla erecta*, *Deschampsia flexuosa*, *Melampyrum hians*, *Oxalis acetosella* and *Pteridium* and *Anthoxanthum* on deeper soils where the slope is less and the soil of pH about 4·0. The ferns included *Blechnum*, *Lastraea oreopteris*, *Dryopteris filix mas* and *Hymenophyllum unilaterale*. The mosses included *Dicranum majus*, *Hylocomium loreum*, *Plagiothecium undulatum*, *Polytrichum commune*, *Dicranum scoparium*, *D. fuscum*, *Hypnum schreberi*, *H. cupressiforme*, *Sphagnum* spp., and *Leucobryum*.

The party then ascended Tilberthwaite Gill. The scree contained *Cryptogramme crispa*, *Saxifraga aizoides*, *Asplenium trichomanes*. The gorge was densely clothed with a scrubby woodland containing abundant woody species, but very little oak. The party did not stay to examine the wood but climbed through it to the *Agrostis-fescue* pastures of the fell top, and as rain began to fall made their way down from the ridge to the Gill.

The sincerest thanks of the Society are due to those who made possible such an interesting and instructive excursion and most of all to the President, whose extraordinary knowledge of the ecology of the area was so unsparingly put at our disposal. We shall remember with great pleasure this most successful of excursions.

H. G.

ANNUAL MEETING AT THE BOTANY SCHOOL, CAMBRIDGE
7–9 January, 1938

Soirée in the Botany School

On the evening of Wednesday, 5 January, between eighty and a hundred members and guests were entertained at a soirée in the Botany School.

A large number of interesting exhibits was shown in the laboratory. Dr A. S. Watt showed a large portion of a bracken rhizome extracted and mounted to exhibit its rooting depth in the soil and its general morphology. This was supplemented by smaller specimens and diagrams. Dr D. H. Valentine showed herbarium and living specimens of British primulas, violas and *Potentilla reptans*, hermaphrodite female plants of *Glechoma hederacea*, and the two sexes of *Petasites vulgaris*, together with a map showing their distribution in the British Isles. Mr M. H. Clifford had set out a collection of mosses from the growing bog surface of the raised bog at Tregaron, Cardiganshire. Dr Butler demonstrated a hygrometer for measuring micro-humidity gradients at the surface of a transpiring leaf under different external conditions of macro-environment. He showed at the same time an evaporimeter for measuring the evaporating power of the air at different heights above, and at various points on, the leaf surface, under different atmospheric conditions. Dr V. M. Conway showed an auxanometer apparatus employed in the field to obtain continuous records of the extension growth of the leaves of *Cladium mariscus*, together with results showing the daily and seasonal drifts of such growth at Wicken Fen. Dr H. Godwin had put out exhibits showing peat samples from various types of blanket bog and raised bog found in this country, and lantern slides illustrating the appearance, structure, and communities of such bogs. In particular there were diagrams showing the stratigraphy of the large raised bog at Tregaron, Cardiganshire. There were also shown examples of the application of pollen-analysis technique to peat deposits at Tregaron, and from the submerged peat beds of the North Sea. Mr G. C. Evans demonstrated a field potometer of the type he employed in ecological measurements in the Nigerian rain-forest, and a controlled condition experimental chamber. Mr P. Falk showed an exhibit illustrating the ecology of central Iceland, a vegetation map of the eastern slopes of the volcano Snaefell, transects and photographs. Dr P. W. Richards put out photographs of vegetation of the Middle Atlas, Morocco, and an exhibit of the growth forms of Bryophyta in tropical rain-forest. Mr Martin showed a vegetation map of the Kalahari sands of Northern Rhodesia, and herbarium specimens from the area. There had also been set out an illustrated account of the itinerary of the Friday excursion, which included an air photograph showing the extinct course of the Little Ouse river meandering as a "roddon" through the peat fens.

The Annual Meeting

The twenty-fourth annual meeting of the Society was held in the Botany School, Cambridge, on the following morning, Thursday 6 January, at 10 a.m., the President, Dr W. H. Pearsall, occupying the chair. The minutes of the previous Annual Meeting were read and confirmed. The report of the Honorary Secretary was read and adopted.

Hon. Secretary's Report for the year 1937

The twenty-third Annual Meeting of the Society was held in the Department of Botany, University College, London, on 9 January. On the evening of Friday, 8 January, about ninety members and guests were entertained to a soirée in the Department, where an exhibit of wide interest had been arranged.

The Annual Meeting was held on the 9th, and after transaction of business six very interesting papers were read to the Society. The warm thanks of the Society are due to Prof. Salisbury and Hill, who gave us the use of their Department and made arrangements for us in the usual generous manner.

The Summer Excursion of the Society was held at the Freshwater Biological Station Laboratory, Wray Castle, Windermere, from 28 August to 1 September. About twenty-five members were present, and took part in excursions to the Lake, to peat bogs, woods and to the local mountain pastures. We are much indebted to the Director and staff of the Station, who spared no trouble to make the meeting so enjoyable, and particularly to our President, Dr Pearsall, who made arrangements for the meeting, and most competently led the excursions.

In the past year two numbers of volume six of *The Journal of Animal Ecology* have been published, appearing in May and November. They contained respectively 238 and 184 pages, thus maintaining the substantial dimensions reached by volume five. Thirty original papers were published with eleven plates, in addition to notes, notices and reviews. Notices of publications on Animal Ecology in this volume totalled 307.

Since the last Annual Meeting there have been issued two numbers of *The Journal of Ecology*, appearing in February and August, and containing respectively 288 and 290 pages, with twenty-five plates. In this volume have been published twenty original papers, as well as notes and book reviews.

The end of this year is marked by the resignation of Prof. Tansley from the editorship of *The Journal of Ecology*. He has edited the *Journal* since the retirement of Dr Cavers. In his capable hands the *Journal* has steadily increased in size and importance, and the Society owes him the profoundest gratitude for his long and valuable service.

The Society's transplant experiments at Potterne are continuing satisfactorily in the hands of Mr Marsden Jones and Dr Turrill.

Since the last Annual Meeting the membership of the Society has risen from 343 to 350. Fourteen members have resigned or have died, and 21 new members have been elected. Of the present membership list 189 members receive *The Journal of Ecology* alone, 111 *The Journal of Animal Ecology* alone, 50 receive both *Journals* and one neither.

During the year the Council of the Society has been asked to interest itself in the National Parks movement, and it has sent representatives to committees called to advance the objects of this movement.

Dr Burtt Davy then spoke of Prof. Tansley's work as editor of *The Journal of Ecology*, paying tribute to the devotion and care with which he had carried out his duties. A vote of thanks to the retiring editor was carried with acclamation. The following elections and resignations were proposed from the chair, and carried *nem. con.*: elected new members, Messrs Dundas, Hope-Simpson, Piemeisel, Burges, Harley, Miss Carey, Mrs Brindley, the Wellington School Natural History Society: resigned, Messrs Eden, Longstaffe, Blair, Gilbert, and Pledge.

The alterations of rules proposed by the Council were explained by the President and Hon. Secretary, and being put from the Chair, were carried *nem. con.* They are as follows:

Rule 8 to read: "The Society shall be governed by a Council of not less than fifteen, and not more than twenty Members, consisting of the Officers of the Society, namely, the President, two Vice-Presidents, the two Hon. Editors, the Hon. Secretary, the Hon. Treasurer, and the Hon. Assistant Treasurer, with ordinary Members of Council."

Rule 14 to read: "The Hon. Assistant Treasurer shall be responsible for collection of subscriptions, shall assist the Hon. Treasurer, shall hold office for three years, and shall be eligible for re-election."

The meeting then proceeded to the election of officers as follows:

President: Prof. A. G. TANSLEY, F.R.S. (retiring, Dr W. H. PEARSALL).

Vice-President: Dr A. C. HARDY (retiring, Prof. SALISBURY).

Hon. Editor Journal of Ecology: Dr W. H. PEARSALL (retiring, Prof. TANSLEY).

Hon. Editor Journal of Animal Ecology: Mr C. S. ELTON.

Hon. Secretary: Dr H. GODWIN.

Hon. Assistant Treasurer: Dr A. S. WATT. (See changes of rules proposed.)

Ordinary Council Members: Dr A. R. CLAPHAM, Mr G. H. BATES, Dr E. W. JONES, Mr C. DIVER, Mr A. D. MIDDLETON, Dr F. T. K. PENTELOW.

Retiring: Dr LEACH, Prof. BOYCOTT, Mr WILMOTT.

Not retiring: Prof. SALISBURY, Mr OLDHAM, Dr RUSSELL, Dr ASHBY.

Dr Pearsall then retired from the chair, and said in so doing how happy the Society was to welcome back to that office Prof. Tansley, who had been its first President, twenty-five years ago. Prof. Tansley, taking the chair, thanked the Society for the honour done him.

The Secretary then outlined suggestions for a single-day meeting at Bedford College at Easter, and for a Summer Excursion at Aberystwyth.

In the absence of further private business the meeting proceeded to the reading of papers.

Capt. C. DIVER described the origin and purpose of the Association for the Study of Systematics, and explained what the Handbooks Committee of that body was doing to correlate the work of Ecology, Genetics, and Cytology with Taxonomic work. He asked for the support of the Society.

Mr J. DUNDAS read a paper on "Vegetation changes in the Sahelian zone of the southern Sahara". He described three main types of vegetation: Savanna thornland, Acacia scrub on indurated soils, and Fringing Forest on the damper soils by water courses. He also described the vegetational zonation round Lake Chad, an interesting example of regeneration of Acacia round new wells, and the marked association of *Tamarindus indica* with the baobab tree. A lively discussion followed, in which Dr Burtt Davy, Dr Godwin, Dr Burges, Mr Middleton, Capt. Diver, Prof. Tansley and Prof. Osborn took part.

Mr J. FORD then read a paper on the food of young partridge chicks, describing the results of crop-analyses from birds of different ages. There was an extremely well-marked change in diet at the end of three weeks, from entirely animal to largely vegetable food. He concerned himself mostly with analysis of the animal food, and drew attention to sources of error in interpreting results based on too few indices of presence. There was evidently much individual variation between birds caused by differing season and opportunity. Capt. Diver, Mr Middleton, Mr Wilmott, Dr Turrill and Mr Blackman took part in the discussion which followed.

Mr J. D. MARTIN then gave an account of the Baikiaea plurijuga forest and other vegetation types of the northern extension of the Kalahari Sands into North Rhodesia. The area lies north-west of the Livingstone Falls, at an altitude of 3000–3500 ft., and has very uncertain rainfall. The soils vary greatly in respect of the relative proportion of fine and coarse materials in them, and therefore in water-retaining power. It was shown how this affected vegetational distribution. Particular interest attaches to Baikiaea plurijuga, the dominant of one extensive forest type, since it is a deciduous, tap-rooted species of a genus otherwise limited to tropical (evergreen) rain-forest. Mr Martin suggested that this forest type had formerly been more widespread than at present, attributing this to climatic change, accelerated by fire, grazing etc. Dr Burtt Davy and Prof. Adamson spoke in the discussion after the paper.

Dr BURTT DAVY then opened a discussion on nomenclature of Forest Communities in the Tropics. He indicated the conflict between existing systems such as those of Chipp and of

Champion, and circulated a draft conspectus for the African forests. The discussion which followed revealed both strong feeling that standardization would be extremely useful, and also a desire not to make premature commitments in instances where principles were not yet understood. Prof. Adamson, Dr A. S. Watt, Dr Richards, Prof. Osborn, Mr Wilmott and Mr Day spoke in the discussion. The meeting finally approved the proposal of the Hon. Secretary that the matter be referred to the Council for consideration by a special committee.

After the adjournment for lunch, the Hon. Treasurer made a provisional statement of the financial position of the Society. This was accepted as satisfactory, and a vote of thanks to the Hon. Treasurer, proposed by the President, was carried unanimously.

It was proposed from the chair, and carried *nem. con.*, that Messrs William Norman and Son be reappointed auditors for the ensuing year. Grants of £5 to the Transplant Experiments of the Society, and of £10 to the Freshwater Biological Association, were similarly approved.

Dr P. W. Richards then gave an account of stratification in a tropical rain-forest with only a single dominant. It was based on work done by Mr T. A. W. Davis of the British Forestry Department, Guiana. Dr Richards showed that the general characteristics of irregular outline, and stratification of woody plants into three or more layers, which is typical of mixed rain-forest, give place to smooth canopy and two storeys of woody plants where there is dominance by a single species. The President and Mr Holttum raised questions afterwards.

Mr P. Falk continued with an illustrated account of the Ecology of Central Iceland. He described mountain slope vegetation on lava soils at about 2000 m. He showed the pronounced effects of varying slope and soil depth, and of snow duration upon the vegetation. The reality of solifluction phenomena was demonstrated by ash-bands due to the volcanic eruption of 1783. In the wetter areas interesting examples of pool and hummock formation were described and the discussion, which followed, turned largely upon this. Mr Marquand, Mr Wilmott, Dr Polunin, Dr Clapham and Dr Turrill spoke.

Dr A. S. Watt then gave an account of some aspects of the autecology of the Bracken fern, concerned with excavation of the rhizome system. He showed how the system is a series of lateral shoots, produced in zig-zag fashion, and though small plants 88 and 68 ft. long had been measured, in another one lateral alone had produced over 200 ft. of rhizome. Dr Watt described the changes of density and rhizome depth across the invasion front of an area of bracken, correlating this with the appearance of the community. In the discussion the President, Mr Baker, Mr Summerhayes, Mr Montford, Dr Turrill, Capt. Diver and Mr Wilmott spoke.

Dr W. H. Pearsall then proposed on behalf of the Society very sincere thanks to Prof. Brooks for having given the hospitality of his department, and for providing the evening soirée. This was carried with acclamation. Dr Pearsall also thanked the Secretary and his assistants for the trouble taken in arranging the meeting.

On the following morning, a party of thirty, under the leadership of Dr Godwin and Mr Tidmarsh, made an excursion by 'bus through the south-eastern fens and the Breckland margin. In the fenland special attention was called to the buried pine forest horizons, the upper and lower peats separated by fen-clay, and the large silt "roddons" which represent the course of extinct rivers in Romano-British to pre-drainage times. The party crossed the Fen-Breck margin between Kenny Hill and Lakenheath, and had lunch on Maidscross Hill overlooking Lakenheath Warren. During lunch Mr Tidmarsh explained the communities visible, and the party then walked across the heath to meet the 'bus on the Brandon road. The party reached Cambridge just after 2.30 p.m.

	£	s.	d.	£	s.	d.	£	s.	d.
Less Prepayments for 1938–9				27	5	0			
				489	13	1			
Less Transferred to *Journal of Animal Ecology* (see below)				195	2	6	294	10	7
Interest on Investments				34	10	0			
Interest on Deposit Account				1	0	4	35	10	4
Journal of Ecology—Sales, etc.:									
Current volume, XXV, 1937				561	18	6			
Back volumes and parts				41	15	1			
Sales of reprints				65	9	6			
Fee for use of photograph				1	1	0			
				670	4	1			
Grants received from:									
University of London	40	0	0						
Ministry of Agriculture and Fisheries	10	0	0						
Government of Mauritius ...	50	0	0	100	0	0	770	4	1
Index Volume, *Journal of Ecology* (vols. I–XX), Sales							30	18	0
Journal of Animal Ecology—Sales, etc.:									
Vol. VI, 1937: Subscriptions received				195	2	6			
Sales				227	5	7			
Sales of reprints				39	13	9			
Vols. I–V: Sales of back numbers				98	6	10			
				560	8	8			
Grant from Carnegie Corporation of New York, through the Bureau of Animal Population, Oxford University				10	0	0	570	8	8
							£1701	11	8

	£	s.	d.	£	s.	d.
Printing, Circulars, etc.	4	12	0			
Postages	8	3	8			
Bank Charges		16	2			
Clerical Assistance (Secretary and Treasurer) ...	15	0	0	28	11	10
Audit Fee				3	3	0
Grant:						
British Ecological Society's Transplant Experiments Fund				5	0	0
Soirée Expenses				3	7	11
Journal of Ecology, vol. XXV (1937):						
Paper, Printing, Illustrations, etc.	736	1	0			
Binding	2	1	0			
Carriage, Insurance, Postages, etc.	48	14	3			
Publishers' Commission	84	4	6	871	0	9
Index Volume, *Journal of Ecology*, vols. I–XX:						
Carriage, Insurance, Postages	6	12	7			
Publishers' Commission	3	1	10	9	14	5
Journal of Animal Ecology, vol. VI (1937):						
Paper, Printing, Illustrations, etc.	508	13	3			
Publishers' Commission	49	3	3			
Carriage, Insurance, Advertising, etc.	27	11	9			
Fee for Special Review	5	0	0	590	8	3
				1511	6	2
Balance, Surplus for the Year				190	5	6
				£1701	11	8

BALANCE SHEET AT 31 DECEMBER, 1937

Liabilities

	£	s.	d.	£	s.	d.
Membership Subscriptions, prepaid for 1938, etc....				27	5	0
Journal of Animal Ecology, vol. VI, pt. 2:						
Printing Account due	221	8	7			
Less Sale of reprints	24	7	6	197	1	1
Library Account				1	5	0
General Revenue Account, Balance of Funds:						
Balance at 31 December 1936	897	5	9			
Add Surplus for year ending 31 December 1937	190	5	6	1087	11	3
				£1313	2	4

Assets

	£	s.	d.	£	s.	d.
Westminster Bank—Credit Balances:						
Current Account	47	9	4			
Deposit Account	350	0	0	397	9	4
Investments:						
£700 3½ % War Loan at cost (Market value at 31 December 1937 at 101½ = £710. 10s. 0d.) ...	717	3	0			
£200 5 % Conversion Loan at cost (Market value at 31 December 1937 at 114½ = £229)... ...	198	10	0	915	13	0
				£1313	2	4

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.

(Signed) WM NORMAN & SONS.
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.

NOTE. A further asset is the unsold Stock of the *Journals* and Index Volumes, held for the Society by the Publishers.

(Signed) HUGH BOYD WATT,

LIST OF MEMBERS (JANUARY 16th, 1938)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

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STUDIES IN THE DISTRIBUTION OF INSECTS BY AERIAL CURRENTS

EXPERIMENTS IN AERIAL TOW-NETTING FROM KITES

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(*With Plates* 8–10 *and* 15 *Figures in the Text*)

CONTENTS

1. INTRODUCTION

DEFINITE migrations are made by a number of the larger flying insects, notably Lepidoptera. Williams (1930), in addition to his own observations, gives a full bibliography of earlier references to insect migration, and recently a study of the migrants into this country has been pursued by the South-Eastern Union of Scientific Societies under the energetic leadership of Capt. T. Dannreuther, R.N., and reported in the *Entomologist* from 1933 onwards. But it is also clear that many of the smaller species must be carried passively by aerial currents: both vertically by convection or other disturbances and horizontally by wind. One of the present authors remembers Mr E. R. Speyer emphasizing the importance of wind drift in the dispersal of the aphid *Chermes* and suggesting in 1920 the tow-netting of the air from aeroplanes. Felt (1925*a*, 1925*b*, 1926, 1928) has discussed such influences at length and collected a large number of examples. Elton (1925) described vast numbers of the aphid *Dilachnus piceae* Panz., and the hover-fly *Syrphus ribesii* Linn. carried on to the ice-cap of North-East Land apparently from the Kola Peninsula, a distance of over 800 miles in a straight line. Uvarov (1931) further discusses the influence of

wind on distribution in his important review of previous work on insects in relation to climate.

The first collections of insects from aeroplanes appear to have been made in America by Coad (1931), who reports on the use of collecting traps up to the height of 14,000 ft.[1] In the following year further experiments in America were made by Collins & Baker (1934).

Travellers at sea have on occasions noticed numbers of insects carried to their vessel when many miles from land. Such an experience one of us (A. C. H.) had on the voyage of the R.R.S. *Discovery* in the autumn of 1925, when a hot wind brought hundreds of insects, large and small, on to the ship from the west coast of Africa more than a hundred miles away.

The following notes are taken from a diary with the midday position of the ship for the dates concerned: 26 October 1925 (16° 23′ 20″ N.; 18° 27′ 15″ W., 130 miles from the African coast): "More insects have come on board to-day than ever before: several butterflies, numbers of moths and beetles and countless grasshoppers, locusts and flying bugs. The latter were a perfect pest, appearing everywhere."

On 13 October (35° 50′ N.; 13° 48′ W., i.e. 310 miles from Portugal and 340 miles from Morocco) I recorded "Spurge hawk moth or allied species, Silver 'Y' moth, other moths and a red admiral butterfly" having come on board; and on 15 October (31° 55′ 30″ N.; 14° 50′ 10″ W., i.e. 295 miles from the African coast) a death's head hawk moth was taken on board.

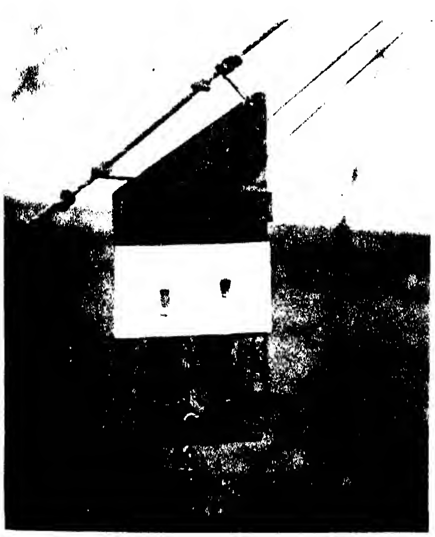
This occurrence at the time when we were engaged in studying the drifting life of the sea, the plankton, led to the development of the methods about to be described; they are an adaptation of oceanographical technique to the study of the "aerial plankton". The process is inverted in the air by sending up kites to support the nets which are opened at the desired height and then closed again before being hauled down, thus ensuring a correct estimation of the small insects drifting at any particular height.

The experiments were begun in May 1932 and continued through the summers of 1933, 1934 and 1935. The senior author (A. C. H.) wishes to make it clear that whilst he directed the experiments and took part in the treatment of the data obtained, the second author (P. S. M.) carried out the greater part of the work in the field and was entirely responsible for the sorting of the collections. The field work in 1935 was carried out by Mr J. A. Freeman who has kindly allowed us to incorporate the material he collected, and will himself contribute a subsequent paper dealing with a more intensive study of insect drift at lower levels which he made in the same year by using collecting nets on the tall masts of a wireless station.

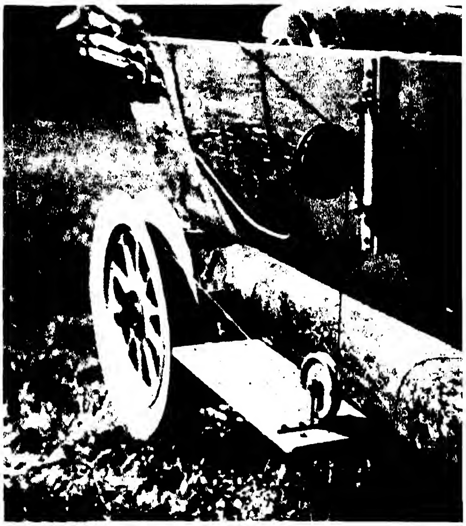
We are indebted to the Agricultural Research Council for a grant of £100 towards the cost of the investigations in 1933. In 1934 and 1935 the work was continued when the second author and Mr Freeman held Ministry of Agriculture Research Scholarships. A brief account of the experiments was given

[1] See Addendum note on p. 226.

Phot. 1. Net going up closed.



Phot. 2. Detail of opening and closing mechanism.



Phot. 3. Kite line leading from spare whee car adapted as power winch.

at the Leicester meeting of the British Association for the Advancement of Science (Milne, 1933) and in the Ministry of Agriculture's *Report on the work of Agricultural Research Institutes* 1932–3 (1934).

Further experiments from aeroplanes using tow-nets instead of traps were begun in France in the summer of 1934 by Berland (1934, 1935, 1936).

The researches described in the present communication form the beginning of a series of investigations, which will form the subject of later papers, on the distribution of insects by aerial currents. A preliminary account of insect drift over the North Sea has already appeared (Hardy & Milne, 1937). During the summers of 1936 and 1937 trial experiments were made with collecting devices on railway trains to obtain series of consecutive samples of insects across the country with a view to investigating the spread of agricultural pests under different weather conditions and the possibility of eventually forecasting such movements.

2. Acknowledgements

We have been most fortunate in securing the kind co-operation of a number of specialists in the identification of our specimens. We are most grateful to Mr N. D. Riley, Keeper of Entomology at the British Museum (Natural History), for his kind interest in this work and to the members of his staff who so generously gave their time to the examination of sections of our collections as follows: Dr K. G. Blair (Coleoptera); Mr W. E. China (Hemiptera, excluding Aphididae); Dr F. W. Edwards (Diptera); Dr G. Ferrière (Hymenoptera).

The naming of Aphididae was undertaken by the second author (P. S. M.) after receiving valuable instruction in methods at the Museum from Mr Laing, who also confirmed his identifications and named some others. Mr E. R. Speyer kindly identified the Thysanoptera, Mr G. J. Kerrich of Cambridge two specimens of Hymenoptera, *Gyrocampa affinis* Nees. and *Hemiteles necator* Grav., and Mr J. V. Pearman a specimen of the psocid *Pterodela pedicularia* Linn.

To all these gentlemen we tender our most grateful thanks.

3. Equipment

Kites, wire and winch

Except in high winds the net is taken up by two kites flown in series. The first is a pilot kite of triangular section box pattern with side wings, having a span of 8 ft. and a height of 8·5 ft. One of similar design but smaller is shown at the top of phot. 5 in Pl. 9. It is easily started in quite light winds and flies very steadily at a good angle. It is connected by 350 ft. of rope to the back of the main lifting kite which is of a double triangular box pattern (see Pl. 9, phot. 4) and specially suitable for use with a pilot. This is 8 ft. across and 5·5 ft. high. About 8 ft. below it are attached the net and its control mechanisms.

This arrangement gives very good results with winds up to force 6 on the Beaufort scale. The two kites, being separated by 350 ft. of rope, combine to smooth out the effects of minor irregularities in the wind and so give a nearly constant angle of pull; whilst the lower kite is experiencing a lull the pilot, further to leeward, may be pulling strongly and so helping to maintain its fellow till the next gust arrives. Longer period variations in the wind velocity cause a slow rising and falling of the whole system which can be overcome to some extent by veering out or hauling in at the right moments.

With winds of force 6 and upwards the pull of the two kites becomes dangerously strong and the pilot kite may be used alone. This eliminates the risk of a breakaway, but the stability of the system is much reduced.

From the net downwards steel piano-wire, $\frac{1}{32}$ in. diameter, is used; it combines the advantages of low wind resistance, light weight (16 lb. per mile length) and high tensile strength, and may be obtained in continuous lengths of a mile or more. The rope and wire are connected by a Dines shackle. Care must be taken to keep the wire well oiled and free from kinks. We have been much helped by consulting Dines' (1903, 1909) accounts of his pioneer meteorological kite investigations, and by receiving valuable advice from his son, Mr J. S. Dines, of the Meteorological Office.

An old Morris Cowley touring car was converted into a simple and convenient power winch. A spare wheel was made into a storage and winding drum, by welding deep flanges on to the rim; it proved sufficiently strong to withstand the strain of more than a mile of wire wound on under tension. The car, which carries all the apparatus to the scene of operations, is run into a position at right angles to the wind, the rear axle is jacked up at one side and the drum substituted for the off-side wheel. Two pulleys, one fixed and the other free to swing through 180° (see Pl. 8, phot. 3), lead the wire out to the kites.

The kites having been launched, the wire is veered out against the foot brake or hauled in by the engine working in reverse gear. The car is prevented from riding off the jack when hauling in, by putting on the hand brake which has been disconnected from the off-side wheel. Care must be taken to avoid putting too great a strain on the wire when hauling in. When the net is being sent to heights over 1500 ft., another lifting kite is attached to the wire so that as much wire again may be carried into the air.

Warning banners, according to Air Ministry regulations, are attached to the wire every 300 ft. to show the position of the wire to passing aircraft pilots.

The collecting net

The net resembles the marine tow-net and is made in three sections: first, a cylinder of very wide mesh netting 20 in. long fastened to a wooden hoop 1 yd. in diameter; secondly, a conical bag of muslin 1 yd. in diameter in front and 3 yd. long tapering to join the third section, which is a small calico

cylinder just big enough to surround a strong glass specimen tube to hold the insects caught. Three whipcord bridles are attached to the hoop. At the junction of the wide mesh netting and the muslin bag is a band of tape round the net, and to the outside of this are sewn at equal intervals twelve small rings. Two separate cords, each arranged as a freely running noose, pass through these rings; one keeps the net closed on ascent until released by the mechanism about to be described, and the other closes the net again for descent after the bridles have been released, also by the action of the mechanism.

The opening and closing mechanism

Originally it was intended to use a clockwork mechanism, and later Mr Freeman constructed such a device, but for the greater part of the time a

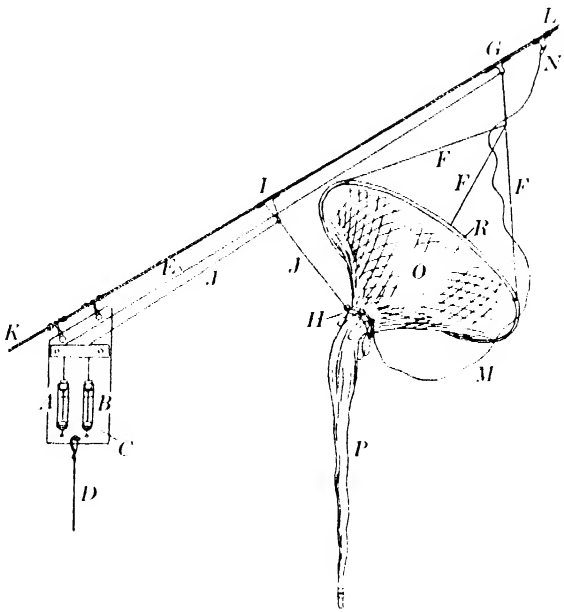


Fig. 1.

very simple, efficient and light chemically controlled mechanism was used and found very satisfactory. It works by the action of nitric acid on copper wire.

The letters in the following description refer to those in Fig. 1; the mechanism is also seen in Pl. 8, phots. 1 and 2. *A* and *B* are two small glass tubes, corked at each end, attached to a plywood board *C* which hangs by brass wires from the kite line *KL*. Each tube has a copper wire passing through it. That passing through the tube *A* is fixed below the tube to the board *C* and fastened above the tube to a cord *E*; this, leading through a guide on the board, is fastened at its other end to the bridles *F* of the net, after having passed through the wire loop *G* which suspends the net from the kite line *KL*. The net is kept closed on ascent by a cord *J* drawn tight through the small rings sewn on the tape round the net at *H*; this cord passes back, through the wire loop *I* on the

kite line, to be fastened to the upper end of the copper wire which passes through the tube *B*. Another cord *M*, also forming a noose through the rings *H*, but left quite slack, is fastened to the kite line at *N*.

The tube *A* is filled with weak acid and the tube *B* with stronger acid, and the apparatus is ready for ascent. On going up the collecting net proper *P* is kept closed by the cord *J* drawn tight through the rings *H*; the part *O* connecting the net proper to the ring *R* is a cylinder of wide open mesh netting which will allow any insects to pass through. Soon after the net has reached the desired height the copper wire in tube *B* is eaten through by the stronger acid so that the cord *J* is released and the muslin collecting net *P* flies open in the wind with the bridles pulling on the cord *E*.

The weaker acid in tube *A* is made up to such a strength that it will eat through its copper wire in approximately 1 hr., 2 hr. or such time as is desired. At the end of this period the cord *E* is released and the net falls to be caught by the cord *M* which tightly throttles the muslin net *P* and so prevents any further capture of insects. The apparatus is now ready for hauling down (see Pl. 9, phot. 5).

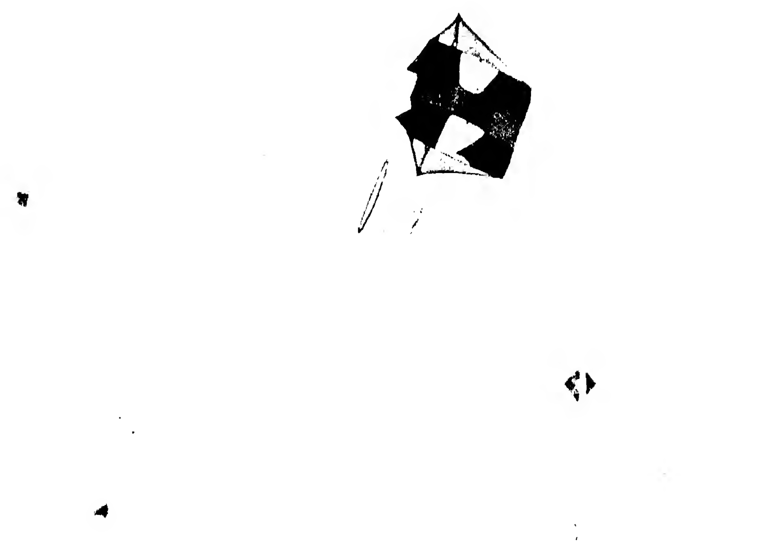
The speed of the acid reaction varies with the temperature, but by using a thermometer as a rough guide to the conditions the operator can after a little experience time the exposure to within a few minutes. The actual duration of the exposure is observed and recorded. With an air temperature near the ground of 20° C. and acids of 50 and 25% strength the net will open in a quarter of an hour, and remain open for 2 hr. The wire used in the fuses was 24 s.w.g. tinned copper.

Lateral movements of the kites tend to swing the fuse board from side to side and may eventually cause it to turn completely round the kite line and entangle the control cords. To prevent this a small lead weight is hung from the lower edge of the board at *D* by about 12 ft. of cord, and its oscillations are damped out by the addition of a baffle consisting of two pieces of plywood interlocking at right angles (see Pl. 8, phot. 1). The lead weight and baffle swing gently to and fro at the end of the cord and ensure the smooth working of the mechanism under all normal working conditions.

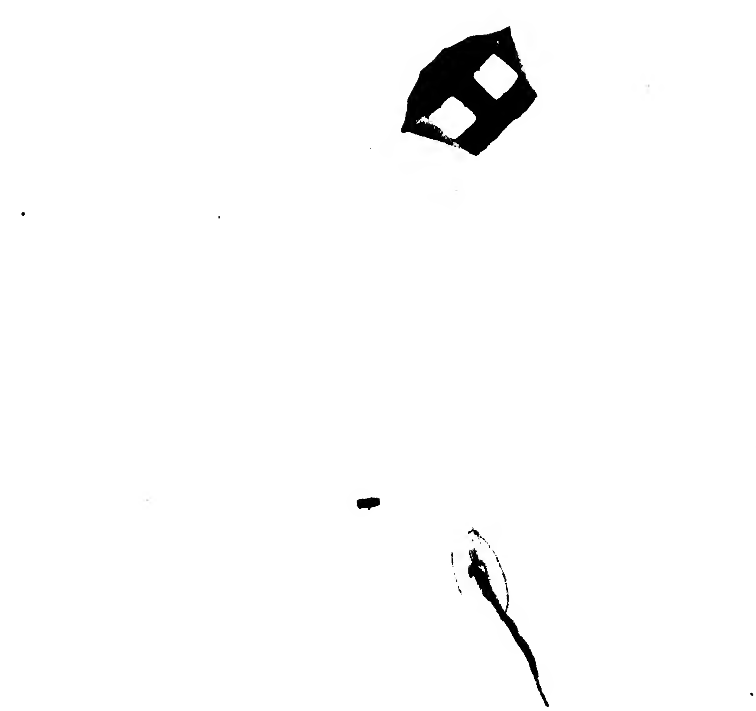
The simplicity and reliability of the method and its ability to withstand the severe buffeting of the wind and weather are compensation for the more precise timing which would be given by a clockwork or electrical device.

4. Method of kite flying

In light winds the pilot kite is started by throwing it into the air at the end of the full length of inter-kite rope (350 ft.), and simultaneously hauling in with the engine, so that the kite rapidly soars to a level where the wind is sufficiently strong to maintain it. The rope is now veered out slowly to the point where it is connected to the main length of piano-wire. Here the second kite is inserted along with the short piece of strong rope supporting the net and



Phot. 4.



Phot. 5.

Phot. 4. Net opened for collecting.
Phot. 5. Net closed prior to hauling down.

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fuse board. When these are correctly adjusted with the net in the closed position ready for ascent the fuse tubes are filled with acid of appropriate strengths by a pipette. (A series of 30 c.c. vials is kept at hand, storing small quantities of nitric acid in strengths varying from 20 to 50%.) The whole system is then veered out as quickly as conditions permit, attaching the red and white warning banners every 300 ft., until the desired height is reached. After the drum is stopped the kites continue to rise for a short period before settling down to a steady angle of flight. After a few minutes the first fuse breaks and the net flies open into the collecting position. (Pl. 9, phot. 4.)

In moderate to fresh winds the pilot kite may be launched at a short distance and the rope veered out immediately without any preliminary hauling in.

During flight the kite is from time to time observed through a small telescope mounted on a quadrant on a levelled tripod so that its height may be calculated from a measurement of the angle of the telescope and a knowledge of the length of wire out, an allowance being made for the catenary curve of the line. The amount of line out is recorded by an adaptation of a cyclometer.

After the closing of the net the wire is hauled in under engine power and the net detached from the kite line as soon as it reaches the ground. The whole of the muslin part of the net, together with the glass tube, is put into a large cyanide killing jar. After death those insects still clinging to the inside of the net are shaken down to join those already in the tube. The inside of the net is searched and any insects which are found *dead* added to the tube; any living insects found are not included, since these might have alighted on the net in the course of examination.

Before the ascent the net is scrutinized to see that no insects have crawled or flown into it before it is closed, and as already explained the wide-mesh netting in front of the closed muslin net allows any insects encountered during ascent to pass through uncaught.

5. Description of experiments 1932–5

The experiments were made during the summer months of the years 1932–5. The particulars of date, position, time and duration of net exposure, height and meteorological conditions and total catch of insects at each station are given in Table 1. The details of the nature of the catch are given in § 6.

The majority of the flights were made at Hull from the playing fields of the University College lying on the N.W. outskirts of the city, where a good exposure to winds in all directions is available. One of the objects of our investigations is to study the infection of this country by small wind-borne insects from abroad, as distinct from the larger true migrants being investigated by others. For this purpose we took the apparatus to the coast of Suffolk at Thorpeness in July 1933, and to the top of the 500 ft. Abbot's Cliff between Folkestone and Dover in July and August of the same year and in

Table 1. *Station list, meteorological observations and records of total catch*

Station number	Date	Position	Time of exposure (G.M.T.)	Duration of exposure (hr.)	Height of net (ft.)	Wind direction, force of wind and state of weather*			Atmospheric pressure in millibars	Temp. °F.	Relative humidity %	Total catch
	1932											
1	18 May	Hull	1530–1645	1¼	150–200	S. by W.	3	c	1021·0	68	55	48
2	19 ,,	,,	1225–1355	1½	150–200	S.S.W.	2	c	1019·4	66	59	31
3	19 ,,	,,	1510–1640	1½	250	S.S.W.	2	c	1018·0	66	59	9
4	19 ,,	,,	1705–1805	1	250–300	S.S.W.	2	c	1017·5	66	59	12
5	2 June	,,	1230–1430	2	200–300	N. by E.	4–5	bc	1018·0	58	64	23
6	2 ,,	,,	1730–1930	2	250–350	N.N.E.	4–3	bc	1018·1	53	68	8
7	7 ,,	,,	1730–1830	1	250–350	W.	3	c	1025·7	58	64	10
8	18 ,,	,,	1730–1900	1½	150–250	N.N.E.	3–4	bcc	1024·5	55	69	3
9	24 ,,	,,	1515–1615	1	200–300	W.	4	c	1022·0	67	55	9
10	29 ,,	,,	1500–1630	1½	200–250	S.S.E.	3	b	1016·5	66	70	5
11	18 July	,,	1230–1430	2	250–350	N.	5	c	1021·0	57	82	2
12	5 Aug.	Aldbrough, E. Yorks	1500–1630	1½	250–300	N.W. by W.	3	c	1022·5	66	65	13
13	15 ,,	Hull	1420–1620	2	250–300	E.	4	c	1023·3	66	60	18
14	17 ,,	,,	1050–1250	2	250–350	W.	3–4	b	1025·0	77	50	7
15	17 ,,	,,	1320–1450	1½	200–350	W.	4	b	1025·0	77	50	14
16	5 Sept.	,,	1350–1550	2	300–350	W.	3–4	c	1014·0	64	73	5
17	6 ,,	,,	1520–1650	1½	300–350	W.	3	bc	1006·5	62	70	4
18	12 ,,	,,	1500–1700	2	350–400	W.	4	bcc	1016·5	61	48	11
19	26 ,,	,,	1240–1420	1½	275–325	W.	3	b, bc, c	1006·0	59	71	3
20	27 ,,	,,	1350–1650	3	300–350	N.	3	bc	1026·0	52	50	9
21	29 ,,	,,	1230–1430	2	300–350	N.E. by E.	4	bc	1024·4	61	67	33
22	29 ,,	,,	1440–1640	2	300–350	N.E. by E.	4	bc	1020·0	58	68	6
23	6 Oct.	,,	1145–1345	2	325–375	S.E. by S.	3	bz	1016·0	58	53	15
24	31 ,,	,,	1355–1555	2	350–375	N.N.E.	4	b	1016·0	45	60	6
	1933											
25	26 April	,,	1450–1530	¾	250–350	S.	3–4	c	1014·2	56	65	1
26	19 May	,,	1430–1600	1½	200–450	S.	2–3	bcz	1022·0	66	55	8
27	29 ,,	,,	1535–1605	½	350–450	N.E. by E.	3–5	bcc, bc	1023·5	54	65	2
28	31 ,,	,,	1545–1645	1	250–350	S. by E.	5	b	1017·6	64	50	18
29	1 June	,,	1430–1555	1½	720–850	S.E.	5–6	bcz	1021·0	64	55	2
30	2 ,,	,,	1440–1540	1	450–500	S.	4–5	bcc, o	1021·0	70	50	16
31	7 ,,	,,	1510–1610	1	200–300	S.E.	3–5	b	1020·0	75	40	9
32	8 ,,	,,	1420–1650	1½	200–500	N.E.	4–5	b, bc, m	1025·0	65	70	14
33	13 ,,	,,	1310–1540	1½	500–600	N.E.	5–6	o, d	1016·5	54	74	0
34	28 ,,	,,	1500–1600	1	300	N.	3–4	bcc	1014·2	65	60	8
35	16 July	,,	1430–1730	3	300–350	N.	6	b	1014·0	65	80	5
36	26 ,,	Thorpeness	1310–1510	2	380–630	S.S.W.	5	b	1017·2	77	65	41
37	26 ,,	,,	1545–1745	2	410–610	S.W.	5	b	1017·0	74	65	34
38	28 ,,	,,	1040–1140	1	150–410	W.	2–5	b	1019·0	70	45	18

39	28 ,,	,,	1330–1430	1	280–480	S.W.	4–5	bbc	1019·2	73	45	15
40	2 Aug.	Abbot's Cliff	1637–1737	1	480	S.W.	6	bcz	1028·0	75	50	8
41	4 ,,	,,	1705–1805	1	150	N.E.	3	bc	1024·7	73	55	7
42	5 ,,	,,	1110–1210	1	350	E.	4–5	b	1024·0	72	55	3
43	5 ,,	,,	1525–1610	$\frac{3}{4}$	450	N.E.	6	b	1023·0	73	70	23
44	8 ,,	,,	1324–1625	3	450	S.W.	4	b, bc, c	1016·4	77	60	39
45	9 ,,	,,	1740–1900	$1\frac{1}{4}$	250–350	S.W.	4	bc	1018·0	68	75	4
46	10 ,,	,,	1320–1350	$\frac{1}{2}$	600	N.W.	5	c	1021·6	76	45	6
47	13 ,,	,,	1150–1420	$2\frac{1}{2}$	350–600	E.	3–4	bc	1023·6	68	45	18
48	13 ,,	,,	1445–1650	2	450–600	E.	6–8	bc, c	1022·0	68	50	14
49	4 Sept.	Hull	1515–1700	$1\frac{1}{4}$	500–1200	N.W. by W.	3–5	bc	1026·3	70	60	6
	1934											
50	2 May	,,	1445–1625	$1\frac{1}{2}$	275–375	E.N.E.	3–4	bc	1013·6	60	60	1
51	3 ,,	,,	1440–1620	$1\frac{1}{2}$	450–550	E.N.E.	3	b	1015·5	52	82	0
52	1 June	,,	1355–1510	$1\frac{1}{4}$	250–350	N.N.E.	3	b	1022·1	64	50	17
53	4 ,,	,,	1430–1500	$\frac{1}{2}$	400–450	N.E. by N.	4–5	c, bbc	1020·5	57	84	0
54	11 ,,	,,	1420–1540	$1\frac{1}{2}$	500–600	N.E.	3–5	b	1019·3	65	70	4
55	27 ,,	,,	1430–1535	1	500–550	W.	3–4	o, bcc	1013·5	70	55	1
56	27 ,,	,,	1610–1640	$\frac{1}{2}$	500–550	W.	3–4	o, bcc	1013·2	65	55	5
57	29 ,,	,,	1500–1610	$1\frac{1}{4}$	500–550	N.E. by E.	3	o, bc, b	1025·0	60	55	5
58	19 July	,,	1055–1310	$2\frac{1}{4}$	400–450	N.W. by W.	5–6	bc	1012·0	70	62	14
59	20 ,,	,,	1440–1540	1	450–500	S.E.	3–4	bcc	1010·0	68	60	13
60	23 ,,	E. Yorks wolds	1500–1600	1	1600–2100	N.W. by W.	3–4	bc	1013·3	72	70	18
61	30 ,,	Abbot's Cliff	1530–1645	$1\frac{1}{4}$	200–750	S.W.	4–2	bcz	1011·5	70	70	0
62	31 ,,	,,	1555–1755	2	600–650	W.S.W.	4–5	c, bc	1008·6	68	75	1
63	1 Aug.	,,	1435–1735	3	450–500	S.W. by W.	4	bcc	1012·1	66	75	0
64	3 ,,	,,	1240–1520	$2\frac{1}{2}$	850–900	S.W.	4	c, bc	1007·0	67	65	0
65	9 ,,	,,	1315–1515	2	800–900	W.	3–4	bc	1013·0	61	90	13
66	9 ,,	,,	1545–1645	1	800–900	W.	3–4	bc	1010·0	60	90	8
67	3 Sept.	Hull	1515–1615	1	800–850	S.W.	4–5	bc	1008·2	65	65	7
68	9 ,,	,,	1640–1755	$1\frac{1}{4}$	650	S.W. by W.	3–4	bc	1010·0	60	78	6
69	10 ,,	,,	1615–1715	1	600–800	S.W.	3–4	b	1020·0	65	85	32
70	18 ,,	,,	1525–1625	1	600–650	S.W.	3–4	bcc	1013·9	65	75	7
71	25 ,,	,,	1515–1645	$1\frac{1}{2}$	550–900	S.W. by W.	3–4	b	1015·0	58	78	11
	1935											
72	9 May	,,	1645–1800	$1\frac{1}{4}$	1650–2240	?	?	b, bc	1006·0	54·5	60	0
73	29 ,,	,,	1600–1700	1	1300–1700	E.N.E.	3–4	?	1001·0	57·0	60	2
74	25 Aug.	,,	1135–1235	1	400–1000	E.	3–4	b	1026·0	82	70	1
75	25 ,,	,,	1510–1725	$2\frac{1}{4}$	950–1500	E.S.E.	3–4	bc	1008·0	86	66	4
76*a*	27 ,,	,,	1435–1705	$2\frac{1}{2}$	850–1250	W.N.W.	3–4	bc	1004·0	67	58	20
b	27 ,,	,,	1600–1630	$\frac{1}{2}$	180–370	W.N.W.	3–4	bc	1004·0	67	58	10
77*a*	30 ,,	Tetney	1350–1620	$2\frac{1}{2}$	400–1400	S.S.W.	6	cr	1005·0	67	60	4
b	30 ,,	,,	1410–1620	$2\frac{1}{4}$	350–800	S.S.W.	6	cr	1005·0	67	60	1
78	1 Sept.	Hull	1600–1730	$1\frac{1}{2}$	450–2350	S.	4–5	bccR	1006·0	74	76	1
79	26 ,,	Cave wold	1645–1815	$1\frac{1}{2}$	550–2000	?	5	?	1008·0	78	74	10
80	2 Oct.	,,	1540–1715	$1\frac{1}{2}$	1550–1750	S.	4–5	?	958·0	53	71	0

* In the Beaufort weather notation.

August 1934. During our visits to the Suffolk and Kent coast we received valuable assistance in the field from Mr R. Liddington. The coast at Thorpeness is low-lying with a shingle beach from which the flights were made, with a hinterland of undulating wold country. Whilst good collections were made at these points, the winds on each occasion for the whole period of our visits were towards instead of from the sea. That aerial currents must be important agents in carrying small insects to this country was, however, demonstrated by the collections made in the summer of 1936 (Hardy & Milne, 1937) when nets were flown from kites and from the mast-head on the Ministry of Agriculture and

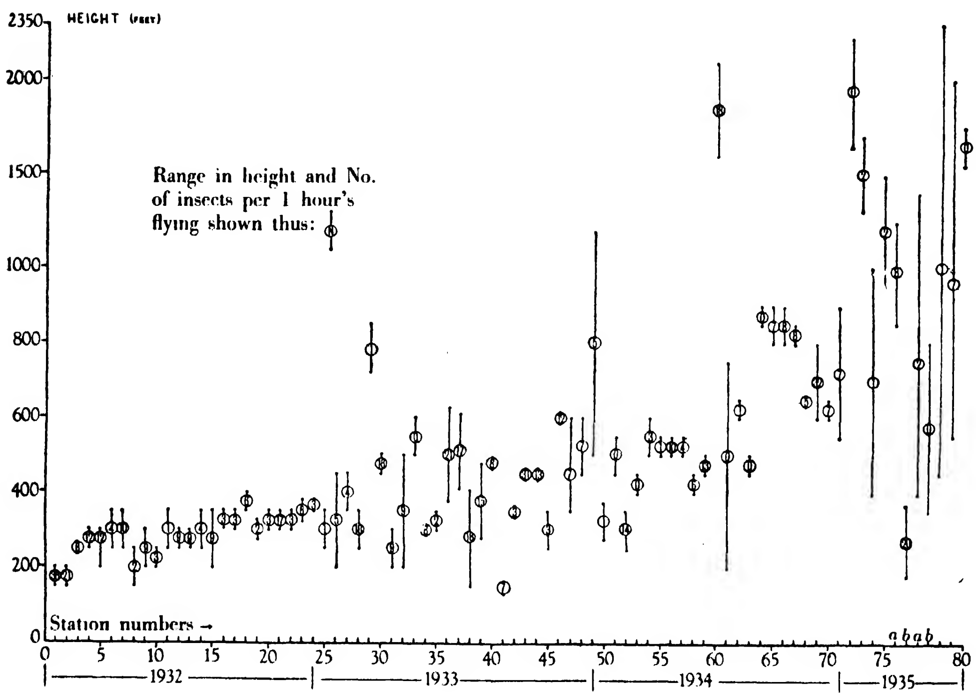


Fig. 2. Chart showing the ranges of height sampled in the series of experiments during the summers of 1932–5 together with the number of insects caught per 1 hr. collecting in each net. The nets were of uniform pattern, 3 ft. diameter opening, and kept closed on the way up and down.

Fisheries research ship *George Bligh* during one of her routine cruises over the North Sea. Numbers of insects were taken at distances between 100 and 150 miles from land. The collections made on the Suffolk and Kent coasts show how vast a population of insects is constantly being swept out to sea.

Other flights were made on the east Yorkshire wolds near Market Weighton and at Cave Wold, at Tetney near Grimsby, and at Aldbrough on the east Yorkshire coast.

The flights in 1932 were made with a simpler technique than that described above. A smaller pilot kite, a rope line and a hand winch were used; the net being opened and closed by pulling a light cord looped up at intervals

to the main line. The weight and wind resistance of the rope line and the smaller lifting power of the pilot kite limited the flights to 450 ft. The automatic net control and power winch were introduced at the beginning of the 1933 season, and the heights reached were gradually increased to over 2000 ft. In 1935 Mr Freeman introduced a clockwise release mechanism to control the opening and closing of the net.

Fig. 2 shows graphically the ranges in height sampled by the nets in the whole series of the experiments. The numbers in the circles represent the numbers of insects taken per 1 hr. collecting during each flight. It is seen that as we extended the height of sampling, it became more difficult to keep the kites at an even level, and a considerable range of varying height was usually experienced in the higher flights. Whilst the greatest height reached was 2350 ft., the highest steady flight was for a period of 1 hr. 25 min. at 1550–1750 ft.

Altogether 82 samples were taken yielding a collection of 839 insects during a total flying time of 124·5 hr.

6. Nature of the aerial plankton

With the exception of the single specimen of the butterfly *Pieris rapae*, all the insects taken belong to families of small- or light-bodied insects with rather weak powers of flight, but with relatively large wing surfaces compared with body mass (see Pl. 10, phots. 6 and 7). They may truly be described as drifting in the aerial currents and so may justly be described as aerial plankton. The Aphididae, of which 250 individuals were taken in our collections, forming 30% of the total insect catch, are particularly well adapted to transit by aerial currents.

Table 2 gives the catches at each station analysed into families, the stations being arranged in order of height (the mean height for each flight) from the highest at the top of the table to the lowest at the foot. This table thus represents a section of the aerial plankton as sampled in our experiments between 150 and 2000 ft. The number of occasions on which each family occurred, together with the total number of individuals of each family, are given at the foot of the table.

The Aphididae, Acalypterae, Mycetophilidae and Chalcidoidea (in order of numerical importance) together form 69·5% of the total collections.

A list of all species identified is given in Table 10 at the end of the paper, together with the stations at which they occurred. Many of those taken in 1935 were not determined beyond the family.

A more general impression of the composition of the aerial plankton may be obtained from Table 3 and Fig. 3, wherein are shown the numbers of the representatives of the more important families taken per 10 hr. collecting at different height ranges up to 2000 ft.

Table 2. *Analysis of samples into families. The samples are arranged in descending order of height. The mean height of each net is given and the range of height may be found on reference to Table 1*

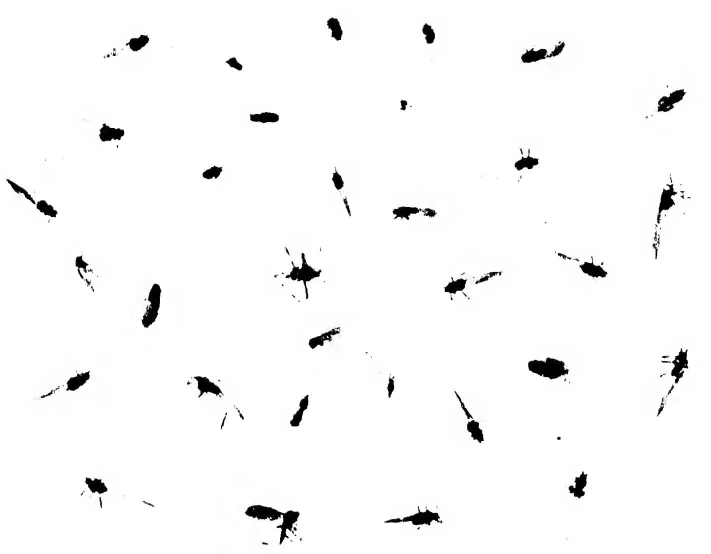
Height of net (ft.)	Station No.	Hemiptera: Psyllidae	Hemiptera: Jassidae	Hemiptera: Aphididae	Thysanoptera	Coleoptera: Staphylinidae	Coleoptera: Chrysomelidae	Diptera: Mycetophilidae	Diptera: Cecidomyidae	Diptera: Chironomidae	Diptera: Agromyzidae	Diptera: Chloropidae	Diptera: Ephydridae	Diptera: Sphaeroceridae	Diptera: Other Acalypterae	Hymenoptera: Ichneumonoidea	Hymenoptera: Chalcidoidea	Hymenoptera: Proctotrypoidea	Other insects	Total catch
1945	72	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
1825	60	.	.	11	1	.	.	.	.	.	.	1	1	.	.	1	3	.	— —	18
1650	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
1500	73	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	— —	2
1400	78	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	— —	1
1275	79	.	1	6	.	.	.	2	.	1		.	.	.	.	.	.	.	— —	10
1225	75	.	1	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.	— —	4
1050	76*a*		.	.	.	.	12	.	.	.	.	2	1	.	.	1	.	3	(Arachnida: Araneida 1)	20
900	77*a*	.	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	1	— —	4
875	64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
850	49	1	.	.	.	.	.	1	.	1	.	.	.	.	.	.	1	1	Psocoptera 1	6
850	65	.	.	1	1	.	.	.	.	1	.	4	.	.	.	1	5	.	— —	13
850	66	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	7	.	— —	8
825	67	.	.	6	.	.	.	.	.	.	.	.	.	.	.	1	.	.	— —	7
725	71	4	.	2	.	.	.	.	.	.	.	.	.	.	.	3	.	.	Diptera, Bibionidae 2	11
700	69	3	.	22	.	1	.	1	.	.	.	.	.	.	1	.	1	.	Psocoptera 3	32
700	74	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	— —	1
675	29	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	— —	2
650	68	.	.	1	.	1	.	.	.	.	.	.	.	.	.	2	1	.	Psocoptera 1	6
625	62	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	— —	1
625	70	.	.	5	.	.	.	.	.	.	.	.	.	.	.	2	.	.	— —	7
600	46	.	.	.	1	.	.	.	.	.	.	3	.	.	.	.	2	.	— —	6
575	77*b*	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	1
550	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
550	54	.	1	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	— —	4
525	48	.	2	1	.	.	.	.	.	.	1	4	.	.	1	.	1	.	Hemiptera: Delphacidae 1 Lygaeidae 1 Diptera: Empididae 1 Phoridae 1	14
525	55	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	1
525	56	.	2	.	.	.	.	.	1	.	.	.	1	.	.	1	.	.	— —	5
525	57	.	3	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	— —	5

500	36	1	.	10	5	.	.	.	.	.	.	.	2	.	.	10	5	3	Hymenoptera, Cynipoidea 5	41
500	37	.	1	9	.	.	.	.	.	.	.	.	1	.	.	4	1	2	Hymenoptera: Cynipoidea 5 Undetermined 11	34
500	51	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
475	30	.	.	12	2	.	.	.	.	.	.	.	.	1	.	.	.	.	Hemiptera, Delphacidae 1	16
475	40	.	.	1	.	.	.	.	.	.	.	1	.	.	.	3	1	1	Diptera, Drosophilidae 1	8
475	47	.	1	2	.	.	.	.	.	.	.	11	.	.	.	.	3	.	Coleoptera, undetermined 1	18
475	59	.	1	3	2	2	.	.	.	.	.	.	.	.	1	.	3	.	Lepidoptera, Pieridae 1	13
475	61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
475	63	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
450	43	.	1	3	.	.	1	.	.	.	.	.	.	.	.	.	12	2	Hemiptera, Delphacidae 1 Hymenoptera, Cynipoidea 1 Diptera: Lonchopteridae 1 Drosophilidae 1	23
450	44	1	.	15	2	.	.	1	.	.	1	4	.	1	.	2	9	.	Neuroptera, Coniopterygidae 1 Hemiptera, Delphacidae 1 Coleoptera, undetermined 1	39
425	53	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	Nil
425	58	.	.	8	3	.	.	.	.	.	.	.	.	.	2	.	1	.	— —	14
400	27	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	— —	2
375	18	.	.	4	.	.	.	2	.	.	.	2	.	.	1	2	.	.	— —	11
375	24	.	.	1	.	2	.	1	.	.	.	.	.	1	.	.	.	.	Diptera, Tipulidae 1	6
375	39	.	1	4	1	.	.	3	.	.	.	.	.	.	.	2	4	.	— —	15
350	23	4	1	7	.	.	.	.	.	.	.	.	.	2	.	.	1	.	— —	15
350	32	.	.	9	.	.	.	1	1	.	1	.	.	.	1	.	.	.	Diptera, undetermined 1	14
350	42	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	— —	3
325	16	.	1	1	.	.	.	1	.	.	.	.	2	.	.	.	.	.	— —	5
325	17	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	1	.	— —	4
325	20	.	.	2	.	.	.	2	.	.	.	1	2	.	.	.	.	.	Diptera: Empididae 1 Drosophilidae 1	9
325	21	.	.	3	.	3	.	4	.	.	.	1	1	6	2	.	5	.	Diptera: Phoridae 7 Drosophilidae 1	33
325	22	.	.	3	.	.	.	.	.	.	.	.	.	1	.	.	2	.	— —	6
325	26	.	.	1	.	3	.	.	2	.	.	.	.	.	1	.	.	.	Diptera, Bibionidae 1	8
325	35	1	1	1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	— —	5
325	50	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	— —	1
300	6	.	.	2	.	1	.	3	.	.	.	.	.	.	.	.	.	.	Diptera: Psychodidae 1 Undetermined 1	8
300	7	.	.	1	.	.	.	.	.	.	.	.	.	.	8	.	.	.	Hymenoptera, undetermined 1	10
300	11	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	Diptera, Cordyluridae 1	2
300	14	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	2	.	— —	7
300	19	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	— —	3
300	25	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	— —	1
300	28	.	.	14	.	.	.	2	.	.	.	.	.	.	1	1	.	.	— —	18
300	34	.	.	3	.	.	.	.	1	.	.	.	2	.	.	1	1	.	— —	8

Table 2 (*cont.*)

		Hemiptera				Coleoptera		Diptera								Hymenoptera				
Height of net (ft.)	Station No.	Psyllidae	Jassidae	Aphididae	Thysanoptera	Staphylinidae	Chrysomelidae	Mycetophilidae	Cecidomyidae	Chironomidae	Agromyzidae	Chloropidae	Ephydridae	Sphaeroceridae	Other Acalypterae	Ichneu-monoidea	Chalcidoidea	Procto-trypoidea	Other insects	Total catch
300	45	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	— —	4
300	52	.	.	1	2	2	.	4	1	1	.	2	.	.	1	1	1	.	Diptera, Empididae 1	17
275	4	.	.	1	.	1	.	5	.	1	.	.	.	.	3	.	.	.	Coleoptera, Hydrophilidae 1	12
275	12	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	1	.	Diptera, Cordyluridae 1 Hymenoptera: Cynipoidea 2 Undetermined 1	13
275	13	1	.	5	.	1	.	8	.	.	.	1	.	1	.	.	1	.	— —	18
275	15	.	.	9	.	.	.	.	.	.	.	2	.	.	.	1	1	1	— —	14
275	38	.	.	4	.	.	.	.	.	.	.	.	.	1	9	.	.	1	Hymenoptera, undetermined 3	18
275	76*b*	.	.	.	.	.	8	.	.	.	.	.	1	.	.	.	1	.	— —	10
250	3	.	.	1	.	3	.	5	.	.	.	.	.	.	.	.	.	.	— —	9
250	5	.	.	.	.	.	.	8	.	.	.	.	6	.	3	.	.	.	Hemiptera, Delphacidae 1 Hymenoptera, undetermined 5	23
250	9	.	1	3	.	.	.	.	.	.	.	.	2	.	.	3	.	.	— —	9
250	31	.	.	5	.	1	.	2	.	.	1	.	.	.	.	.	.	.	— —	9
225	10	.	.	2	.	.	.	.	.	1	1	1	.	.	.	.	.	.	— —	5
200	8	.	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	— —	3
175	1	.	.	17	.	1	.	19	.	.	.	.	.	.	7	.	.	.	Diptera: Rhyphidae 1 Lonchopteridae 1 Muscidae 1 Undetermined 1	48
175	2	.	.	4	.	2	.	15	.	.	.	.	.	.	6	1	.	.	Diptera: Empididae 1 Hymenoptera, undetermined 2	31
150	41	.	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	Diptera: Drosophilidae 1 Sepsidae 1 Hymenoptera, Cynipoidea 1	7
Totals: No. of occurrences		8	23	55	10	18	6	23	6	7	7	19	14	8	18	21	30	9	— —	
No. of individuals		16	28	250	20	30	24	92	7	7	7	45	24	14	50	45	79	15	86 (including 1 spider)	839

Phot. 6. Sample of aerial plankton taken in a 3 ft. diam. net during an hour's collecting at 1600–2100 ft. at Station 60 (see Table 1).



Phot. 7. Sample of aerial plankton taken in a 3 ft. diam. net during an hour's collecting at 600–800 ft. at Station 69 (see Table 1). Magnification as in phot. 6.

Table 3. *Number of insects per* 10 *hr. collecting at different height ranges*

Height in ft.	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneu-monoidea	Chalcidoidea	Other insects	Total
1000–2000	2·4	14·4	0·0	11·2	1·6	4·0	1·6	0·0	1·6	2·4	4·8	44·0
750–1000	1·0	8·0	0·0	1·0	1·0	4·0	0·0	0·0	2·0	13·0	8·0	38·0
500–750	5·0	16·5	2·0	0·0	1·0	4·5	0·5	2·0	4·0	2·5	10·5	48·5
250–500	1·8	22·3	2·3	1·3	5·4	3·7	1·7	7·9	4·1	8·3	17·4	76·2
150–250	0·8	28·6	8·2	0·0	40·0	0·8	7·3	16·3	3·3	0·0	11·6	116·9
Total	11·0	89·8	12·5	13·5	49·0	17·0	11·1	26·2	15·0	26·2	52·3	323·6

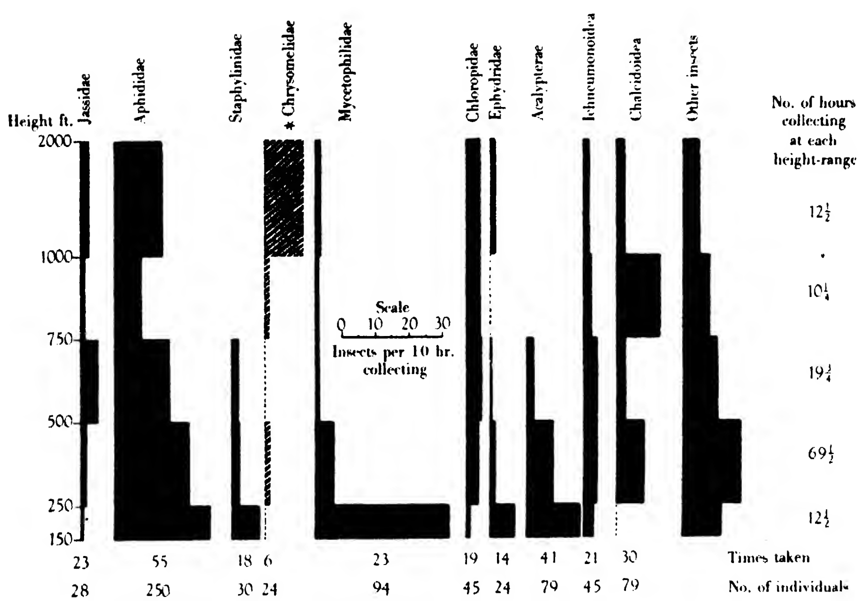


Fig. 3. Graphic representation of the composition of the aerial plankton between 150 and 2000 ft. The blocks represent the average number of insects of different families taken in each height range per 10 hr. collecting (from Table 3). The numbers of individuals and the number of occurrences on which they are based are given below the figure. The chrysomelid figures are largely influenced by observations at one station (see text).

In Table 4 the vertical distribution of each of these same families is shown by expressing the average numbers of any one family per 10 hr. collecting at each height range, as a percentage of the total of that family taken (per 10 hr. collecting) at all height ranges. The results are shown graphically in Fig. 4, where the families are rearranged in a series passing from those with lower to those with higher vertical distributions. The total numbers of insects of each family on which the calculations are based are shown below the name of the family. The apparent irregularity in vertical distribution in some families is no doubt due to the paucity of the data available; nevertheless, we obtain a

good general indication of the relative heights usually reached by the different families.

Table 4. *Percentage distribution over ranges of height for each of the more important families (each column totalling* 100 *vertically)*

Height in ft.	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneumonoidea	Chalcidoidea	Other insects	All insects
1000–2000	21·8	16·0	0·0	83·0	3·3	23·5	14·4	0·0	10·7	9·2	9·2	13·6
750–1000	9·1	8·9	0·0	7·4	2·0	23·5	0·0	0·0	13·3	49·6	15·3	11·7
500–750	45·4	18·4	16·0	0·0	2·0	26·5	4·5	7·6	26·7	9·5	20·1	15·0
250–500	16·4	24·8	18·4	9·6	11·0	21·8	15·3	30·2	27·3	31·7	33·3	23·5
150–250	7·3	31·9	65·6	0·0	81·7	4·7	65·8	62·2	22·0	0·0	22·1	36·2

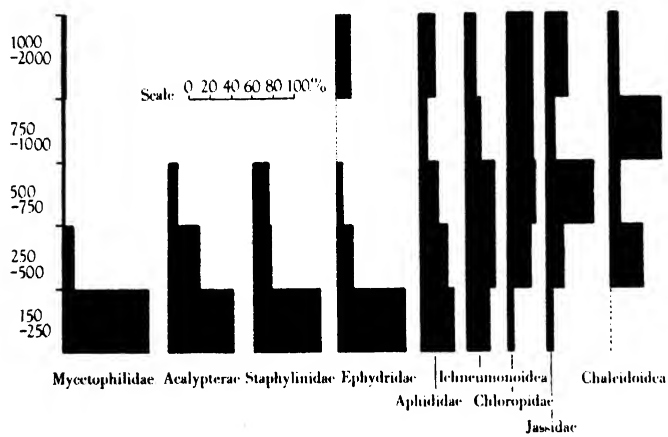


Fig. 4. Chart showing the percentage distribution of the more important families at different height ranges arranged from left to right in ascending order of height distribution (see Table 4).

The comparative uniformity in distribution of the Aphididae, Ichneumonoidea and Chloropidae up to 2000 ft. is well brought out. The surprising distribution of the Chrysomelidae is omitted from Fig. 4: it must be taken with reserve, since it is based on only six occurrences and 24 individuals of which 20 were taken on the same day (27 August 1935).

In Table 5 the numbers of the representatives of these same families are shown as *percentages of the total catch* of all insects per 10 hr. collecting *at each height range*. From this we may see the relative percentage composition of the aerial plankton within each height range. Above 100 ft. the Aphididae, Chrysomelidae (see qualification above), Chloropidae and Chalcidoidea are the more important elements. Estimates of the density of the aerial drifting insect populations are given in § 8.

A comparison may be made here between the results of our experiments and those made by collecting from aeroplanes by Collins & Baker (1934) in America, and by Berland (1935) in France. Coad, who made aeroplane

Table 5. *Percentage composition of the aerial plankton within each height range (each line totalling* 100 *horizontally)*

Height in ft.	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneu-monoidea	Chalcidoidea	Other insects
1000–2000	5·5	32·7	0·0	25·5	3·6	9·0	3·6	0·0	3·6	5·5	11·0
750–1000	2·4	21·1	0·0	2·6	2·6	10·5	0·0	0·0	5·2	34·2	21·4
500–750	10·3	34·0	4·1	0·0	2·1	9·3	1·0	4·1	8·2	5·1	21·8
250–500	2·4	29·3	3·0	1·7	7·1	4·9	2·2	10·4	5·4	10·9	22·7
150–250	0·7	24·4	7·0	0·0	34·2	0·7	6·2	13·9	2·8	0·0	10·1

collections in America (1931), gives no details of his catches[1]. Collins & Baker, using opening and closing screens, in May 1932 caught 25 insects during 9 flights between 300 and 5000 ft., and in May 1933, caught 28 insects during 14 flights between 500 and 3000 ft. Berland in 1934, using nets instead of screens, caught 38 insects during 12 flights (June to September) at heights varying from 1500 to 7000 ft. The following is a list of the families recorded by them; the letters "C & B" and "B" indicate whether they were taken by Collins & Baker or by Berland, and the letter "K" is also added against those families which were taken in our kite-net experiments.

COLLEMBOLA	Sminthuridae	B		—
THYSANOPTERA	—	B	—	K
PSOCOPTERA	—	B	—	K
HEMIPTERA	Capsidae	—	C & B	—
	Jassidae	B	—	K
	Psyllidae	B	C & B	K
	Aphididae	B	—	K
COLEOPTERA	Carabidae	—	C & B	—
	Staphylinidae	—	C & B	K
	Byrrhidae	—	C & B	—
	Helodidae	—	C & B	—
	Chrysomelidae	B	—	K
LEPIDOPTERA	Lymantriidae (Gipsy moth larvae)	—	C & B	—
DIPTERA	Tipulidae	—	C & B	K
	Chironomidae	—	C & B	K
	Cecidomyidae	B	C & B	K
	Mycetophilidae	—	C & B	K
	Bibionidae	—	C & B	K
	Empididae	—	C & B	K
	Lonchopteridae	—	C & B	K
	Phoridae	—	C & B	K
	Ephydridae	B	C & B	K
	Chloropidae	B	C & B	K
	Sphaeroceridae	—	C & B	K
	Heleidae	B	—	—
	Cypselidae	B	—	—
HYMENOPTERA	Braconidae	B	C & B	K
	Chalcididae	B	C & B	K
	Proctotrypidae	—	C & B	K
ARACHNIDA	—	—	C & B	K

Particularly interesting are the specimens of gipsy moth larvae (*Lymantria dispar*) taken by Collins & Baker (one specimen at 2000 ft.) and the collembolan *Bourletiella lutea* by Berland between 3250 and 4000 ft.

[1] See Addendum note on p. 226.

The following is a list of those species or related species which are common to two or all three collections together with the heights at which they were taken; the letters C & B, B, and K indicate the collections as before.

Psyllidae: *Aphalara* sp. C & B, 2000; *A. calthae* Linn. K, 500.

Jassidae: *Deltocephalus pascuellus* Fall. B, 3900; K, 350.

Chloropidae: *Oscinis (Oscinella) frit* Linn. C & B, 2000; K, 600.

Lonchopteridae: *Lonchoptera lutea* Fall. C & B, 500; K, 450.

Ephydridae: *Hydrellia flaviceps* Mg. B, 3250; *H. griseola* Fall. B, 4900; *H. incana* Stenh. K, 300.

Braconidae: *Aphidius nigripes*, C & B, 1500; *Aphidius* sp. K, 480.

Chalcididae: *Cyrtogaster vulgaris* Walk. C & B, 2300; K, 410.

The results of all three collections emphasize the fact that the aerial plankton is essentially made up of weak flyers of small size with a large surface-weight ratio. In the case of our kite-net experiments the method of collecting by means of a net suspended passively in the air is definite evidence that the insects at the time of their capture were being carried along by the prevailing air currents and that they were not engaged in making independent directional flights. In order to test whether strong-flying insects might be caught, but subsequently escape from our nets, such insects as bluebottles, wasps and bees were on several occasions placed (uninjured and in good condition) in the net before the ascent; in every case the insects were found to be still in the net at the end of the exposure along with the catch proper.

7. Influence of weather conditions

There can be no doubt that marked differences in weather conditions must have an important effect on the numbers of insects being carried in the aerial currents. In a flight made at Hull on 13 June 1933 (Station 33), in an easterly wind of 20–25 m.p.h., the net was flying between 500 and 600 ft. just under the cloud base (at times just within it), where the air was saturated with moisture; the catch for 1·5 hr. collecting was nil. This may be contrasted with the four flights made at Thorpeness on 26 and 28 July of the same year (Stations 36–39), when the wind was westerly and rather variable, averaging some 15 m.p.h., and the weather was hot and sunny towards the end of a period of anticyclonic conditions. Here the catches were 21, 17, 18 and 15 insects per hour's collecting.

Altogether 82 flights were made, but these varied greatly in height. It is desirable to compare the insect catches of as many flights as possible with their differing weather conditions, but clearly we must not compare those taken from widely different height ranges. We may conveniently divide the series of flights into five arbitrary height ranges as follows:

Above 1000 ft.:	8	flights totalling	12·5 hr.
751–1000 ft.:	6	,,	10·25 ,,
501–750 ft.:	15	,,	19·75 ,,
251–500 ft.:	44	,,	69·5 ,,
150–250 ft.:	9	,,	12·25 ,,

In one height range alone, that from 250 to 500 ft., we have a sufficient number of flights to make a general correlation with weather conditions worth while. All the following correlations are confined to this series of 44 flights giving a total of 69·5 hr. collecting. The flights were usually of 1 hr. duration each, but sometimes they were longer and on a few occasions were less. Throughout the

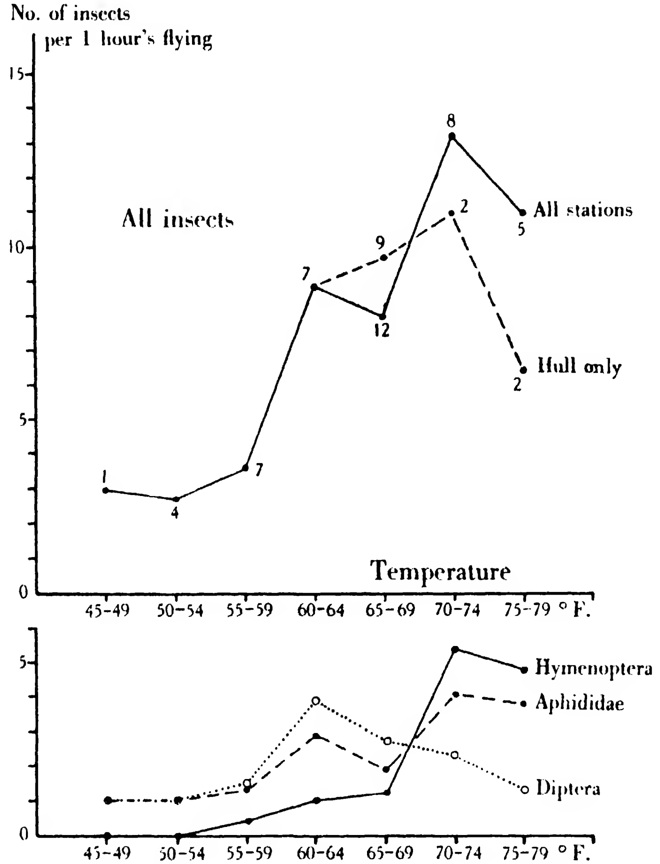


Fig. 5. Curves showing the average number of insects per 1 hr. collecting within the height range of 250–500 ft. at different ranges of temperature from 45–79° F. The numbers against the points on the curves represent the number of observations averaged in each temperature range. The Aphididae, Hymenoptera and Diptera curves are based on all stations; in the case of total insects the Hull observations are in addition shown separately.

following calculations the number of insects caught per flight have, where necessary, been converted to numbers per 1 hr. collecting.

Fig. 5 shows the correlation of the numbers of total insects, aphides, Diptera and Hymenoptera with a scale of temperature. The curves represent the average number of insects for the flights made within different temperature ranges; the numbers of flights averaged in each range are shown as figures against the curves. Of the 44 flights concerned 32 were made at Hull; of the remainder 4 were made at Thorpeness and 8 at Abbot's Cliff. In the case of the total

insects where the curve for the Hull flights differs from that of all the flights it is shown as a separate broken-line curve. Fig. 6 shows in a similar manner a correlation with a scale of percentage humidity. In the total insects we see clearly a general rise with temperatures up to 70–74° F., followed by a slight falling off of numbers at higher temperatures, and we see a general fall in numbers with increasing percentage humidity. The aphides show a moderate correlation with increasing temperature and a less regular inverse correlation

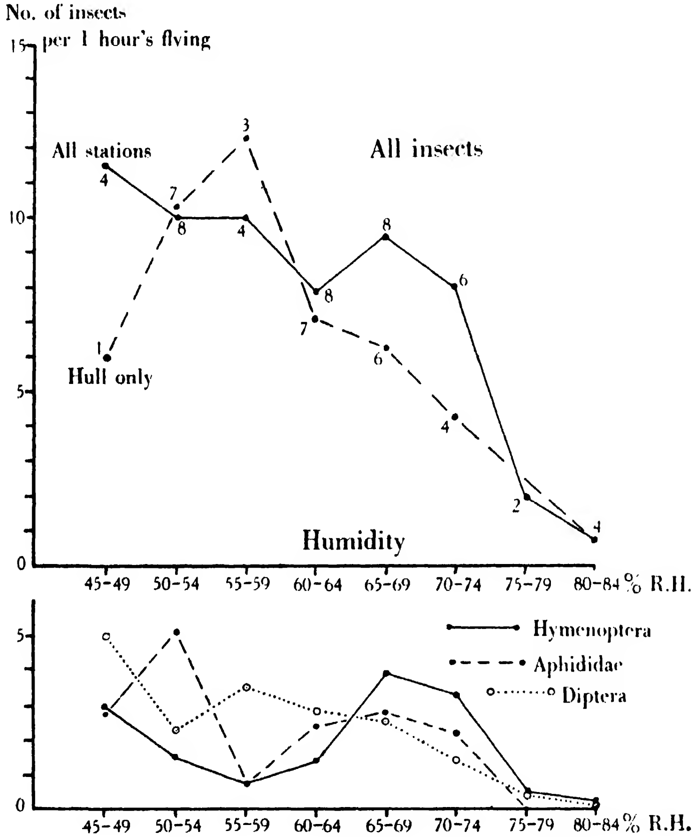


Fig. 6. Curves showing the average number of insects per 1 hr. collecting within the height range of 250–500 ft. at different ranges of percentage relative humidity from 45–84 %. The arrangement is similar to that of Fig. 5 for temperature.

with increasing humidity. The Diptera appear to be more definitely correlated with humidity than with temperature and the Hymenoptera clearly the reverse.

Figs. 7–10 show the influence of temperature and humidity taken together on total insects, aphides, Diptera and Hymenoptera respectively. The dots in the figures represent the relation of the different flights to the two scales of temperature and percentage humidity. The numbers against each dot are the number of insects taken in each flight (per 1 hr. collecting). A thin horizontal line is drawn across the figure to separate 22 of the flights in a higher range of

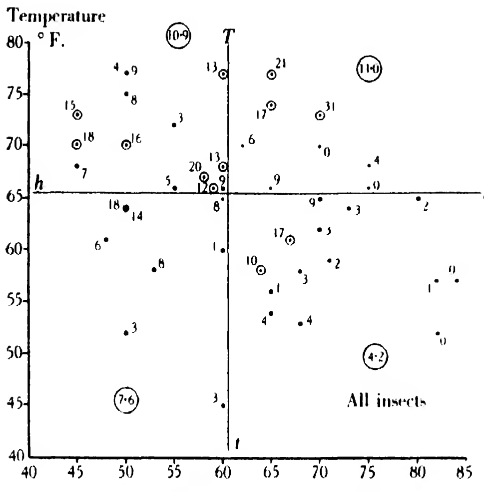


Fig. 7.

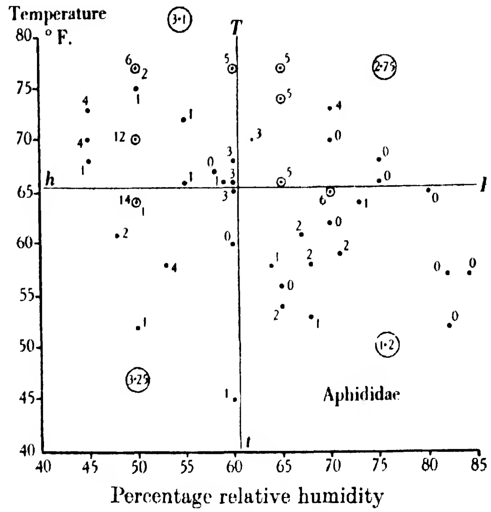


Fig. 8.

Fig. 7. Temperature-humidity diagram. The points in the diagram represent the position of each station within the 250–500 ft. height range in relation to the temperature and humidity scales. The number against each point stands for the number of insects taken per 1 hr. collecting at each station. When this number exceeds 10 the point is given prominence by being surrounded by a circle. The four numbers in circles represent the average number of insects per 1 hr. collecting taken within the area between the intersecting lines *Tt* and *hH* which divide the figure into regions of high and low temperature and humidity.

Fig. 8. Temperature-humidity diagram with similar arrangement as Fig. 7 but for Aphididae only, and with catches of 5 and over given prominence.

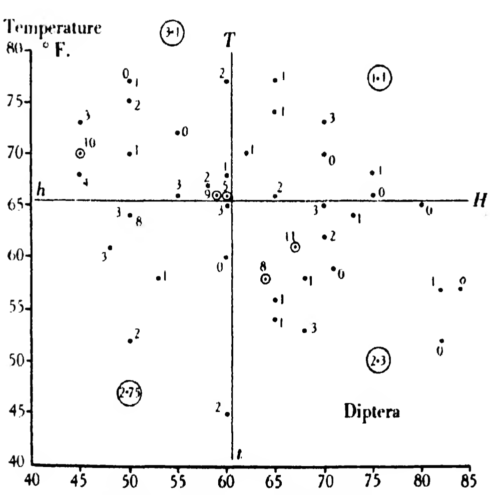


Fig. 9.

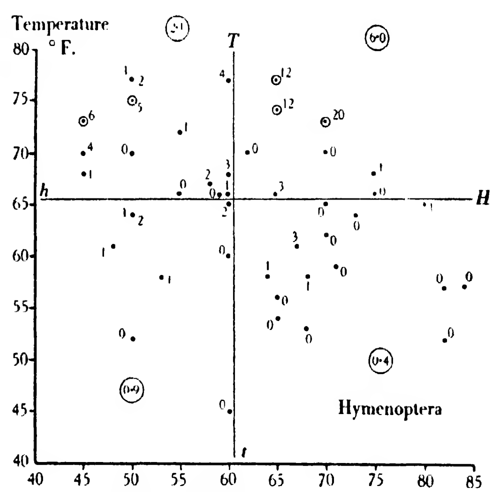


Fig. 10.

Fig. 9. Temperature-humidity diagram with similar arrangement as Fig. 8 but for Diptera only.

Fig. 10. Temperature-humidity diagram with similar arrangement as Fig. 8 but for Hymenoptera only.

temperature from 22 in a lower range of temperature; this line cuts the temperature scale at 65·5° F. Similarly, a vertical line separates 22 of the flights in a higher range of humidity from 22 in a lower range of humidity; this cuts the humidity scale at 60·5 %. These two lines, *Tt* and *hH*, divide the figure into four regions which for convenience may be referred to as *Th*, *TH*, *th* and *tH* (*T* and *t* indicating high and low temperature, *H* and *h* indicating high and low humidity). It so happens that the contrasting squares *Th* and *tH* have each 14 observations in them, so that *TH* and *th* each have 8 observations.

We may now compare the average number of insects taken in each area. Let us first contrast the average number taken in the areas *Th* and *tH*:

	Th	*tH*
All insects	**10·9**	4·2
Aphididae	**3·1**	1·2
Diptera	**3·1**	2·3
Hymenoptera	**2·1**	0·4

We see in each case that *Th* is more favourable than *tH*. Now let us contrast *th* with *TH*.

	th	*TH*
All insects	7·6	**11·0 (9·0)***
Aphididae	**3·25**	2·75
Diptera	**2·75**	1·1
Hymenoptera	0·9	**6·0 (3·75)***

* Omitting 16 chalcids (i.e. 12 for $\frac{3}{4}$ hr. collecting at Station 43).

This latter comparison has not the same weight as that of the other pair of conditions, since these are based on only eight observations in each as against fourteen in the other pair. The same caution must be applied to the following consideration: if we refer across from one pair to the other we see that for each insect group *th* is more favourable than *tH* and that whilst *Th* is more favourable than *TH* for aphides and Diptera, it is not so for Hymenoptera and total insects. If we exclude the one high catch of chalcids at Station 43 then for the total insects $Th > TH$. These results are summarized graphically in Figs. 11–14. Here the lines *Tt* and *hH* cutting at right angles represent the lines *Tt* and *hH* in Figs. 7–10. The values for the average numbers of insects taken in the areas *Th*, *TH*, *tH* and *th* are plotted along the diagonals outwards from the point of their intersection. The plotted points are now connected to make polygons, which may be compared to give an indication of the respective behaviour of the different insect groups in relation to temperature and humidity. These figures based on only a small number of examples must be regarded as only a preliminary indication of the comparative trends.

Bright sunshine might be a factor influencing the flight of insects and so their passage to higher levels by rising currents, but on the present data it is not easy to separate the effect of sunshine from temperature and humidity. In Table 6 are given the average numbers of insects per 1 hr. collecting between

250 and 500 ft. when the conditions were sunny (b, bz, or bbc : 14 instances), partly sunny (bc, bcz: 16 instances) or cloudy (bcc, c: 13 instances). The average temperatures and percentage humidity for these conditions are also

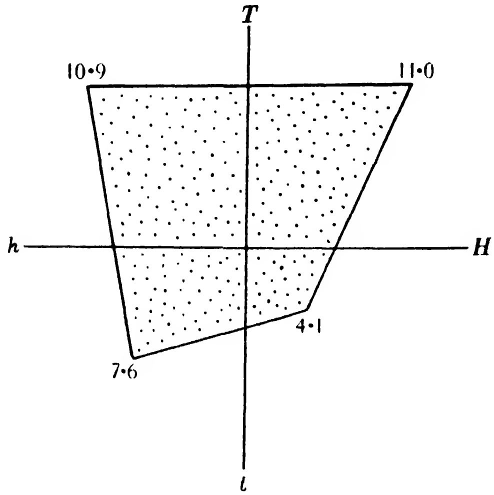


Fig. 11.

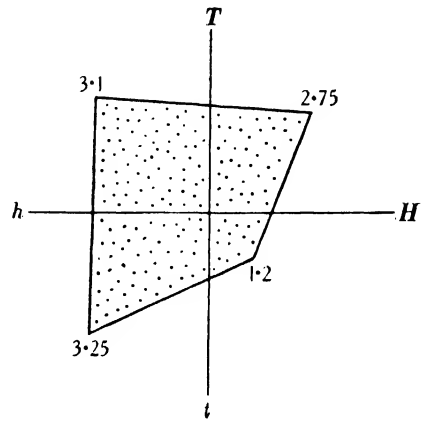


Fig. 12.

Fig. 11. Temperature-humidity relations for total insects (see text).
Fig. 12. Temperature-humidity relations for Aphididae (see text).

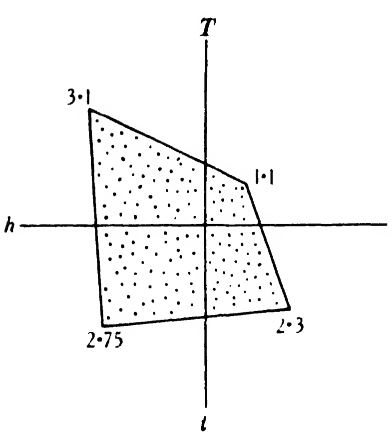


Fig. 13.

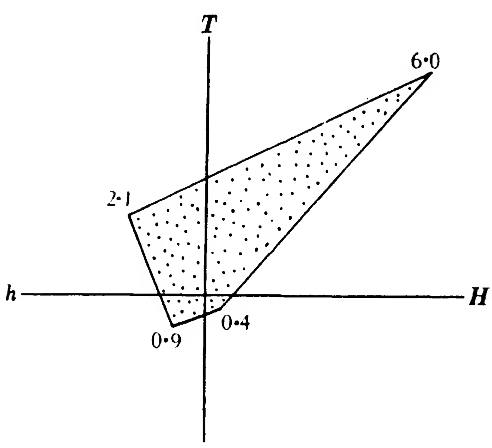


Fig. 14.

Fig. 13. Temperature-humidity relations for Diptera (see text).
Fig. 14. Temperature-humidity relations for Hymenoptera (see text).

given. Whilst we see that higher numbers are taken for all insect groups in sunshine, the accompanying temperature is highest and humidity lowest.

There appears to be no significant correlation between the numbers of insects taken and barometric pressure, as shown in Table 7, and there are not

sufficient data to make a correlation with wind force. The kites could not be flown in very light or high winds; the majority of flights were made in winds of force 3–4, only two flights in this height range (250–500 ft.) were in winds below force 3 and only four above force 5. Data on the influences of wind will be published by Mr Freeman in his forthcoming paper on the results obtained with nets flown on the masts of a wireless station.

Table 6. *Average number of insects per* 1 *hr. collecting under conditions of sunshine or cloud* (250–500 *ft.*)

	(b, bz, bbc)[14]	(bc, bcz)[16]	(bcc, c)[13]
Total insects	**11·6**	6·6	7·1
Aphides	**3·6**	2·3	2·5
Diptera	**3·1**	2·3	2·8
Hymenoptera	**4·6**	1·1	0·8
Av. temp. ° F.	**67·2**	64·4	62·3
Av. % humidity	58·6	62·4	**63·4**

Table 7

Barometric pressure in mb.	Average number of insects per 1 hr. collecting
<1010	8·3[3]
1010–1014·9	3·8[9]
1015–1019·9	10·7[13]
1020–1024·9	9·2[13]
>1024·9	7·2[6]

8. Estimates of the drifting insect populations

An early attempt to measure the density of the insect population of the lowest stratum of the air was made by Bonnet (1911), who made collections with a net attached to the front of a motor car. He found that the average density of the population at this level varied from 0 to 150 per cu.m. of air, depending upon time of day, temperature and humidity of the air.

Weiss, Felt and others (see Uvarov, 1931) studied the insects at slightly higher levels, and proved that the population of the respective strata of the atmosphere must be very rich in numbers, but the first estimate of the magnitude of the population was made by Coad (1931). He found that the number of insects in a vertical column of air 1 mile square and extending from 50 to 14,000 ft. above the ground averaged 25,000,000 throughout the year at Tallulah, Louisiana, the population being lowest in January at 12,000,000 and highest in May at 36,000,000. Details of the collections and the figures on which the estimates are based were not given[1].

In Table 8 is given the average number of insects taken per 10 hr. collecting with our kite-nets at various height ranges between 150 and 2000 ft. These results are shown graphically in Fig. 15, together with results kindly supplied to us by Mr Freeman from his collections in nets of similar size flown from the masts of the Tetney wireless station in Lincolnshire. The two sets of data form

[1] See Addendum note on p. 226.

Table 8

Height ranges in ft.	Hr. collecting	Average number of insects per 10 hr. collecting in a 3 ft. diameter net
1000–2000	12·5	44
750–1000	10·25	38
500–750	19·75	48
250–500	69·5	73
150–250	12·25	117

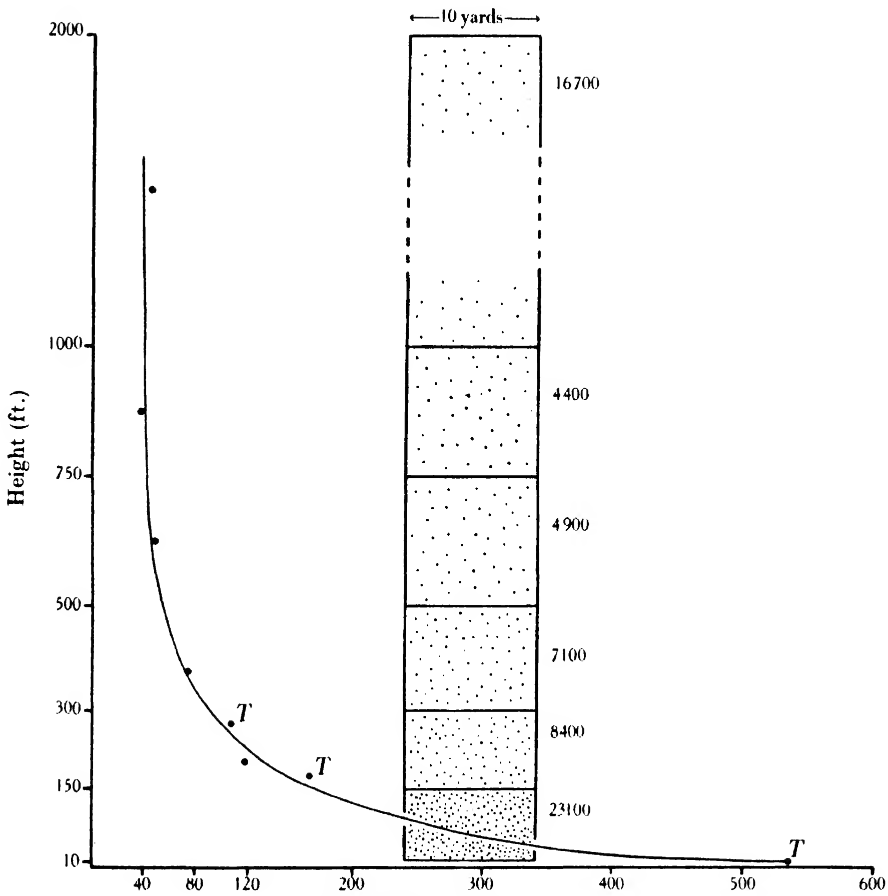


Fig. 15. Graphic representation of the density of the aerial plankton at different heights up to 2000 ft. The curve is based on the number of insects taken per 10 hr. collecting by kite-nets and at the points marked *T* by nets flown from the masts of the Beam Wireless Station at Tetney, Lincolnshire. In addition the average numbers of insects estimated to be drifting over a 10 yd. frontage in 1 hr. within different height ranges are shown by a system of dots, each dot representing 100 insects.

a regular curve and clearly indicate the average density of the aerial plankton from just above ground-level to 2000 ft. The rapid falling off in numbers between 10 and 300 ft. is most marked, yet the numbers at the higher altitudes are

considerable. Superimposed on the curve we also show relative population densities at different heights by a series of dots, each dot representing 100 insects drifting across a 10 yd. frontage in an hour within the different height ranges.

These results show us clearly how much aerial food there is available for swifts and swallows. The behaviour of these birds in respect to height of flight on different days, i.e. flying high on warm dry days and low on cooler damper days, is in accordance with the correlations we have found between temperature and humidity and the numbers of air-borne insects.

Berland (1935) makes a division between a more densely populated "zone terrestre" extending from 1 to 300 m. and a less densely populated "zone planctonique" from 300–5000 m.; but in a subsequent paper (1936) he would place this division between the zones much lower, not higher than 100 m. Our results agree well with this.

To compare with Coad's estimates we can express our results as numbers of insects within each height range in a column of air 1 mile square, estimated on a basis of an average wind velocity during our experiments of 12 m.p.h. This is done in Table 9, where also are given the estimated numbers of insects per 10^6 cu.ft. of air in each height range. Coad's estimates for the whole column of air from 50 to 14,000 ft. when converted into average numbers per 10^6 cu.ft give a minimum of 69 in January and a maximum of 92 in May. These estimates are very high compared with ours.

Table 9

Height ranges in ft.	Estimated number of insects in column of air 1 mile square	Estimated number of insects per 10^6 cu.ft.
1000–2000	245,000	9
750–1000	65,000	9
500–750	72,000	10
300–500	104,000	18
150–300	123,000	29
10–150	339,000	87

9. Economic importance of insect drift by wind

The results of these experiments, together with the collections made over the North Sea (Hardy & Milne, 1937), from which it was shown that insects may be carried for distances of more than 150 miles, would seem to indicate clearly the importance of convection currents and wind drift in the distribution of insect pests from one part of the country to another and the infection of this country by pests brought from the continent.

In the present experiments the grain aphis (*Macrosiphum granarium* Kby.) was taken on 12 occasions and reached a height of 1600 ft. Other aphides listed as agricultural pests by the Ministry of Agriculture and Fisheries were taken up to the following heights: *Capitosphorus ribis* Linn. (410 ft.), *Macrosiphum pisi* Kalt. (1600 ft.), *M. rosae* Linn. (380 ft.), and *Myzus persical* Subz. (650 ft.).

The thrips, *Kakothrips robustus* Uzel., was taken up to 450 ft.; and of the frit-fly (*Oscinus frit* Linn.) 33 specimens were taken on 12 occasions up to 600 ft.

10. SUMMARY

1. The insects carried by convection currents and wind, the aerial plankton, are investigated between the heights of 150 and 2000 ft. by collecting nets carried up by kites. The nets are sent up closed, opened automatically at the desired height, and closed again at the end of the sampling period before being hauled down.

2. The equipment and methods of working are fully described.

3. Eighty-two samples were taken yielding a collection of 839 insects during a total flying time of 124·5 hr.

4. The aerial plankton is made up essentially of small or light-bodied insects with weak powers of flight but with relatively large wing surface compared with body mass.

5. The composition of the aerial plankton at different heights is determined and the height distribution of the different families compared. A list of species identified is appended.

6. The influence of weather conditions is examined. Different insect groups are shown to be affected somewhat differently, but high temperature and low humidity are found for all to be more favourable to aerial drift than the reverse conditions.

7. The average density of the drifting population is estimated for different height ranges up to 2000 ft.

8. The economic significance of insect drift is discussed.

REFERENCES

Berland, L. (1934). "Étude en avion de la faune entomologique aérienne." C.R. Acad. Sci., Paris, 198: 2201–3.

Berland, L. (1935). "Premier résultats de mes recherches en avion sur la faune et la flore atmosphériques." Ann. Soc. Ent. Fr. 104: 73–96.

Berland, L. (1936). "L'Exploration biologique de l'Atmosphère en avion et l'emploi possible de cette méthode en Météorologie." Météorologie, 3rd ser., No. 1: 28–35.

Bonnet, A. (1911). "Recherches sur les causes des variations de la faunule entomologique aérienne." C.R. Acad. Sci., Paris, 152: 336–9.

Coad, B. R. (1931). "Insects captured by airplane are found at surprising heights." Yearb. U.S. Dep. Agric. 1931: 320–3.

Collins, C. W. & Baker, W. L. (1934). "Exploring the upper air for wind-borne gipsy moth larvae." J. Econ. Ent. 27: 320–3.

Dines, W. H. (1903). "The method of kite-flying from a steam-vessel, and meteorological observations obtained thereby off the West coast of Scotland." Quart. J. R. Met. Soc. 29: 65–85.

Dines, W. H. (1909). "Contributions to the investigation of the upper air. Report on apparatus and methods in use at Pyrton Hill." London Meteorological Office, M.O. 202: 15–46.

Elton, C. S. (1925). "The dispersal of insects to Spitsbergen." Trans. Ent. Soc. Lond.: 289–99.

Felt, E. P. (1925a). "The dissemination of insects by air currents." J. Econ. Ent. 18: 152–8.

Felt, E. P. (1925b). "Dispersal of butterflies and other insects." Nature, Lond., 116: 365–8.

Felt, E. P. (1926). "The physical basis of insect drift." Nature, Lond., 117: 754–5.

Felt, E. P. (1928). "Dispersal of insects by air currents." Bull. N.Y. St. Mus. 274: 59–129.

Hardy, A. C. & Milne, P. S. (1937). "Insect drift over the North Sea." Nature, Lond., 139: 510–11.

Milne, P. S. (1933). "The distribution of insects by currents at various levels in the atmosphere." Rep. Brit. Ass.: 489.

Williams, C. B. (1930). "The migration of butterflies." Edinburgh.

Uvarov, B. P. (1931). "Insects and climate." Trans. Ent. Soc. Lond. 79: 97–8, 116–19.

ADDENDUM

Since going to press we learn that Dr P. Glick has made a detailed study of all the material collected on the flights initiated by Dr Coad (see pp. 200, 215 and 222) and that his results are now ready for publication.

APPENDIX

Table 10. *List of species identified in the collections* 1932–5. (*Only a few of the insects collected in* 1935 *have been determined specifically.*) *The names of the specialists responsible for the identifications in different groups are given on p.* 201. *The species listed as pests by the Ministry of Agriculture and Fisheries are marked with an asterisk*

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
PSOCOPTERA		
Pterodela pedicularia Linn.	49 (1)	500–1200
THYSANOPTERA		
Frankliniella intonsa Trybom	36 (1♀), 39 (1♀), 46 (1♀), 60 (1♀)†	250–2100
F. tenuicornis Uzel.	36 (1♀), 58 (1♀), 59 (1♀)‡	380–630
**Kakothrips robustus* Uzel.	30 (2♂), 58 (1♀)	400–500
Limothrips cerealium Halid.	36 (2♀), 52 (1♀), 59 (1♀)	250–630
L. denticornis Halid.	52 (1♀)	250–350
Sericothrips staphylinus Halid.	44 (1♀)	450
HEMIPTERA		
Lygaeidae		
Cymus claviculus Fall.	48 (1)	450–600
Jassidae		
Athysanus plebejus Fall.	48 (1)	450–600
Cicadula sexnotata Fall.	9 (1), 14 (1), 16 (1), 17 (1), 23 (1), 39 (1)	325–480
Deltocephalus pascuellus Fall.	42 (1)	350
D. pulicaris Fall.	35 (1), 77*a* (1)	400–1400
D. socialis Flor.	43 (1)	450
D. striatus Linn.	79 (1)	550–2000
Limotettix quadrinotata F.	45 (1)	250–350
Mocydia crocea H. S.	47 (1)	350–600
Stictocoris preyssleri H. S.	48 (1)	450–600
Delphacidae		
Kelisia vittipennis J. Shulb.	43 (1)	450
Liburnia pellucida F.	5 (1), 30 (1), 44 (1)	450–500

† Contained an egg ready to be laid. (Note by E. R. Speyer.)

‡ The posterior margin of the 8th abdominal tergite is indistinct, so that the insect might possibly (but improbably) be *F. intonsa* Trybom. (Note by E. R. Speyer.)

Table 10 (*cont.*)

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
Psyllidae		
Aphalara calthae Linn.	13 (1), 23 (4), 49 (1)	500–1200
Psyllia nigrita Zett.	36 (1), 44 (1)	450–630
Aphididae		
Anoecia corni Fab.	39 (1), 44 (1), 60 (1)	1600–2100
Anuraphis helichrysi Kalt.	2 (2), 9 (1), 23 (5), 27 (1), 28 (11), 30 (7), 31 (3), 32 (5), 37 (4)	450–610
Anuraphis sp.	9 (2), 39 (2), 41 (1), 42 (1), 47 (1)	350–600
**Capitophorus ribis* Linn.	37 (1)	410–610
Drepanosiphum platanoides Sch.	3 (1), 19 (3), 23 (2), 30 (2)	450–500
Euceraphis betulae Linn.	2 (2), 4 (1)	250–300
Hyadaphis sp.	32 (1)	200–500
Hyalopterus sp.	31 (1), 37 (1), 60 (1)	1600–2100
**Macrosiphum granarium* Kby.	15 (1), 28 (1), 30 (1), 36 (2), 37 (1), 38 (1), 43 (1), 44 (7), 47 (1), 48 (1), 59 (3), 60 (1)	1600–2100
M. pelargonii Kalt.	20 (1), 22 (1), 31 (1), 32 (1), 34 (1), 35 (1), 60 (7)	1600–2100
**M. pisi* Kalt.	36 (1)	380–630
**M. rosae* Linn.	32 (1)	200–500
Megoura viciae Kalt.	39 (1), 40 (1), 44 (1)	450–480
Myzocallis sp.	34 (1)	300
**Myzus persicae* Sulz.	26 (1), 44 (1)	450
	68 (1), 70 (1)	650
Myzus sp.	34 (1)	300
Pemphigus bursarius Linn.	18 (1), 44 (1)	450
Periphyllus sp.	28 (1)	250–350
Rhopalosiphoninus tulipella Theob.	28 (1)	250–350
Therioaphis tiliae Linn.	36 (2)	380–430
NEUROPTERA		
Conopterygidae		
Conwentzia psociformis Curt.	44 (1)	450
LEPIDOPTERA		
Pieridae		
Pieris rapae Linn.	59 (1)	450–500
COLEOPTERA		
Staphylinidae		
Atheta analis Grav.	31 (1)	200–300
A. angustula Gyll.	3 (1)	250
A. nigripes Thoms.	21 (1)	300–350
Exaleochara morion Grav.	2 (1)	150–200
Oxypoda umbrata Gyll.	13 (1)	250–300
Oxytelus nitidulus Grav.	1 (1), 2 (1), 4 (1)	250–300
O. rugosus F.	3 (1)	250
Philonthus varius Gyll.	74 (1)	400–1000
Tachyporus chrysomelinus L.	41 (1)	150
T. hypnorum F.	41 (1)	150
T. pusillus Grav.	21 (1)	300–350
Hydrophilidae		
Helophorus brevipalpis Bed.	4 (1)	250–300
Chrysomelidae		
Longitarsus luridus Scop.	43 (1), 75 (1), 76*a* (12), 76*b* (8), 78 (1)	950–2350
L. suturellus Duft.	77*a* (1)	400–1400

Table 10 (*cont.*)

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
HYMENOPTERA		
Ichneumonoidea		
Aphidius sp.	2 (1), 9 (1), 28 (1), 35 (1), 36 (6), 37 (3), 39 (1), 40 (1)	480–630
Biosteres rusticus Hal.	15 (1)	200–350
Blacus ruficornis Nees.	40 (1)	480
Canidia sp.	36 (1), 44 (1)	450–630
Dacnusa areolaris Nees.	34 (1)	300
Ephedrus plagiator Hal.	37 (1), 44 (1)	450–610
E. validus Hal.	18 (1), 35 (1), 39 (1)	350–480
Gyrocampa affinis Nees.	9 (1)	200–300
Hemiteles necator Grav.	18 (1)	350–400
Homotropus sp.	36 (1)	380–630
Chalcidoidea		
Aphidencyrtus aphidivorus Mayr.	12 (1)	250–300
Asaphes vulgaris Walk.	14 (1), 21 (1), 22 (1), 36 (2), 45 (1), 46 (1)	600–630
Cirrospilus sp.	34 (1), 36 (1), 40 (1), 44 (1), 46 (1)	600–630
Cyrtogaster vulgaris Walk.	37 (1), 47 (1)	410–610
Pachyneuron sp.	23 (1), 49 (1)	500–1200
Panstenon oxylus Walk.	39 (1)	280–480
Pleurotropis sp.	15 (1), 37 (1), 43 (2), 44 (1)	450–610
Pteromalus sp.	36 (1), 43 (7), 44 (2), 47 (2)	450–630
Stenomalus sp.	43 (1), 48 (1)	450–600
Tetrastichus sp.	36 (1)	380–630
Cynipoidea		
Alloxysta filicornis Cam.	36 (2), 37 (2)	410–630
Alloxysta sp.	37 (1)	410–610
Charips victrix Westw.	36 (2), 37 (2)	410–630
Proctotrypoidea		
Conostigmus dubiosus K.	49 (1)	500–1200
Conostigmus sp.	43 (1)	450
Lygocerus aphidivorus Kieff.	15 (1)	200–350
L. serricornis Bov.	36 (1)	380–630
Lygocerus sp.	36 (1), 43 (1)	450–630
Platygaster mayetiolae K.	36 (1), 37 (2), 40 (1)	480–630
*Trichosteresis förster*i Kieff.	38 (1)	150–410
DIPTERA		
Mycetophilidae		
Sciara spp.	1 (19), 2 (15), 3 (5), 4 (5), 5 (8), 6 (3), 13 (8), 16 (1), 18 (2), 20 (2), 21 (4), 24 (1), 27 (1), 28 (2), 31 (2), 32 (1), 39 (3), 44 (1), 49 (1), 52 (4), 54 (1), 69 (1), 79 (2)	500 600–2000
Bibionidae		
Dilophus febrilis L.	26 (1)	200–450
Cecidomyidae		
Camptomyia sp.	34 (1)	300
**Contarinia* spp.	26 (1), 32 (1)	200–500
Chironomidae		
Metriocnemis longitarsus Goet.	4 (1)	250–300
Tanytarsus sp.	49 (1)	500–1200
Psychodidae		
Psychoda phalaenoides L.	6 (1)	250–350

Table 10 (*cont.*)

Order, family, species	Station numbers followed by the number of individuals taken on each occasion	Highest range of height recorded in ft.
Rhyphidae		
Rhyphus punctatus Fab.	1 (1)	150–200
Tipulidae		
Trichocera saltator Harris	24 (1)	350–375
Empididae		
Tachydromia sp.	2 (1), 20 (1), 48 (1)	450–600
Lonchopteridae		
Lonchoptera lutea Fall.	43 (1)	450
Phoridae		
Megaselia sp.	21 (7), 48 (1)	450–600
Agromyzidae		
Agromyza scutellata Fall.	44 (1)	450
Agromyza sp.	48 (1)	450–600
Cerodonta denticornis Pz.	32 (1)	200–300
Phytomyza flava Fall.	10 (1), 11 (1), 17 (1)	300–350
Chloripidae		
**Oscinis frit* Linn.	10 (1), 13 (1), 15 (2), 18 (2), 20 (1), 21 (1), 44 (4), 45 (1), 46 (3), 47 (11), 48 (4), 52 (2)	600
Siphonella sp.	40 (1)	480
Cordyluridae		
Scatophaga stercoraria L.	11 (1), 12 (1)	250–350
Drosophilidae		
Drosophila fenestrarum Fall.	20 (1), 21 (1), 43 (1)	450
Scaptomyza graminum Fall.	40 (1), 41 (1)	480
Ephydridae		
Hyadina guttata Fall.	34 (1)	300
Hydrellia incana Stenh.	5 (6), 8 (1), 9 (2), 16 (2), 17 (1), 20 (2), 34 (1), 76*b* (1)	300–350
Scatella stagnalis Fall.	21 (1), 36 (2), 37 (1), 76*a* (1)	850–1250
Sepsidae		
Sepsis cynipsea L.	41 (1)	150
Sphaeroceridae		
Copromyza equina R. D.	24 (1), 30 (1)	450–500
C. hirtipes R. D.	21 (2), 23 (1)	325–375
Leptocera fontinalis Fall.	21 (1)	300–350
Leptocera spp.	13 (1), 21 (3), 22 (1), 23 (1), 38 (1), 44 (1)	450
Muscidae		
Delia sp.	1 (1)	150–200

MIGRATIONS OF THE SILVER-Y MOTH (*PLUSIA GAMMA*) IN GREAT BRITAIN

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(*With 7 Figures in the Text*)

1. Introduction

Whenever the factors influencing the size and composition of animal populations are under consideration, the possibility of migration from one area to another should not be overlooked. This is usually recognized fully enough in the case of birds and mammals, but it is too often neglected in the case of insect faunas.

None the less, in the sense of the apparently wilful movement of large numbers of individuals for long distances independently of the direction of the wind, migration has been observed in several orders, notably in Lepidoptera and Odonata.

One reason for past neglect of the subject lies in the fact that many entomologists have found it difficult to believe that insects possess the intricate mental or instinctive organization necessary to enable them to undertake deliberate migrations, and so have never looked out for them. As a result, migrations have only been recorded when they have been dense enough to force themselves on the attention of all who came in contact with them. In temperate climates they tend to be ignored altogether, being usually thin and inconspicuous, although careful observation shows them to be frequent.

During the past few years, the situation has much improved. An Insect Immigration Committee has been set up by the South Eastern Union of Scientific Societies, and, thanks largely to the energy and enthusiasm of its Secretary, Capt. Dannreuther, R.N., it is now receiving help from naturalists in all parts of the country, including the keepers of many lighthouses and lightships. Since the majority of the observers are amateurs, Lepidoptera have naturally received the most attention, and as far as some of the species belonging to this order are concerned, fairly solid progress has already been made in various directions.

British migratants have been divided into three groups, according to their relationship to permanent fauna:

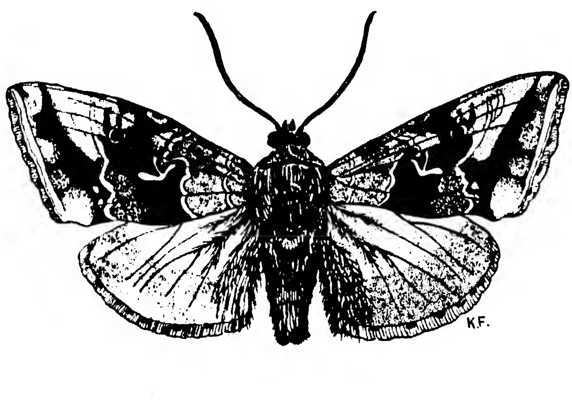
Class A. Species which are unable to pass the winter here, but which appear every summer. They only occur in Great Britain as a result of their migratory habit, and would disappear from the fauna should the migrations cease. Example: *Vanessa cardui* L.

Class B. Species which survive the winter and form part of the normal fauna, but whose numbers are reinforced by immigration. Example: *Pieris rapae* L.

Class C. Species which are normally absent, but which may occur occasionally as vagrants. Example: *Argynnis lathonia* L.

These divisions have been found useful, but they are by no means final; Classes A and B, for example, having a tendency to merge into one another. The difference between Classes A and C, however, does seem to correspond roughly to two different types of migration, though certain insects may behave as Class C in this country which are Class A elsewhere.

As a result of the information so far collected by the Insect Immigration Committee, it begins to look as if the movements of the Class A insects correspond very closely with those of swallows and similar birds. The species concerned appear regularly every spring in considerable numbers, and breed in



Natural size

Fig. 1.

this country. Their offspring reach maturity in late summer and autumn, and in many if not most years the autumn emergences are more numerous than the spring arrivals. Finally in some of the Class A species, *a return flight southwards seems to occur in autumn*, making the migrations a normal and intelligible part of the life of the species, instead of an inexplicable aberration.

The other type of movement, represented by Class C, is more like that of the lemmings. Arrivals are very irregular, and may take place only at long intervals. A British born generation may or may not reach maturity; no return flights are to be expected, and the "migration" would seem to be nothing more than an overflow of surplus population from the normal breeding area.

The present paper is an attempt to deal with a Class A migrant, and while the results so far obtained are not conclusive, they are at least consistent with the suggestions put forward above.

The silver-Y moth, *Plusia gamma* L., has been chosen for this study largely because of the amount of attention it has received from observers under the

Insect Immigration Scheme. It is one of our commonest Lepidoptera, is easy to recognize, and is familiar to every entomologist, yet it is practically never recorded in winter time. Very rarely single specimens have been caught as late as November, like solitary late swallows, but although swarming thousands may be present at the beginning of October, they disappear suddenly about the middle of the month, and except for occasional solitary individuals in November not a trace of them is seen again until the following spring.

There seems to be no doubt that the vast majority of individuals emerge from the pupa in late summer or autumn, and that the winter is passed in the imaginal form. It is exceptional for oviposition to take place in autumn, and all females sent to me for dissection late in the year have had minute ovaries with undeveloped eggs and a copious fat body, characteristics of a species which is to pass the winter in the adult state and will not be ready for oviposition until long after most of the food plants have died down for the winter. If, therefore, the species was not a migrant, but remained in Great Britain, we should expect the majority of insects caught during the winter to be in the adult form and not in the pupal state. This, however, is not the case. Winter records have been especially asked for by the Insect Immigration Committee; only two have been received of insects found from January to April during the past six years, and both of these were pupae. It is difficult to obtain information about the life history of the species abroad, but it is believed to be continuously brooded in warmer climates.

2. Distribution in Great Britain from 1932 to 1936

The information received from the Insect Immigration Committee during the past five years may conveniently be summarized in this section; distribution in three years is illustrated in Figs. 2 (1934), 3 (1935), 4, 5 and 6 (1936).

1932. The first *P. gamma* to be reported in 1932 was seen in Beckley, Sussex, on 19 May, and the main body of immigrants appeared about three weeks later. During June and July moderate numbers were seen in southern England, and as far north as the south Lancashire coast; emergence of the summer generation appears to have begun about the first week in August. Even when allowance is made for the fact that the Insect Immigration Scheme was still in its infancy in 1932 and that observers were fewer than in later years, this emergence does not seem to have been much more numerous than the spring migrants except in one or two places in the south, where the moths were common in August. By the end of the month they had already begun to decrease in number, though a few were seen well on into October, and a single individual was reported from Worcestershire as late as 3 November. No directional movements were recorded in 1932.

1933. The first immigrant was seen on 4 May, a fortnight earlier than in the previous year, and the summer generation was also rather early, emergences taking place from 15 July on. Nevertheless, the year was a bad one for the

species as a whole, and the moths were only seen in numbers in one or two restricted localities. The most northerly point from which they were reported

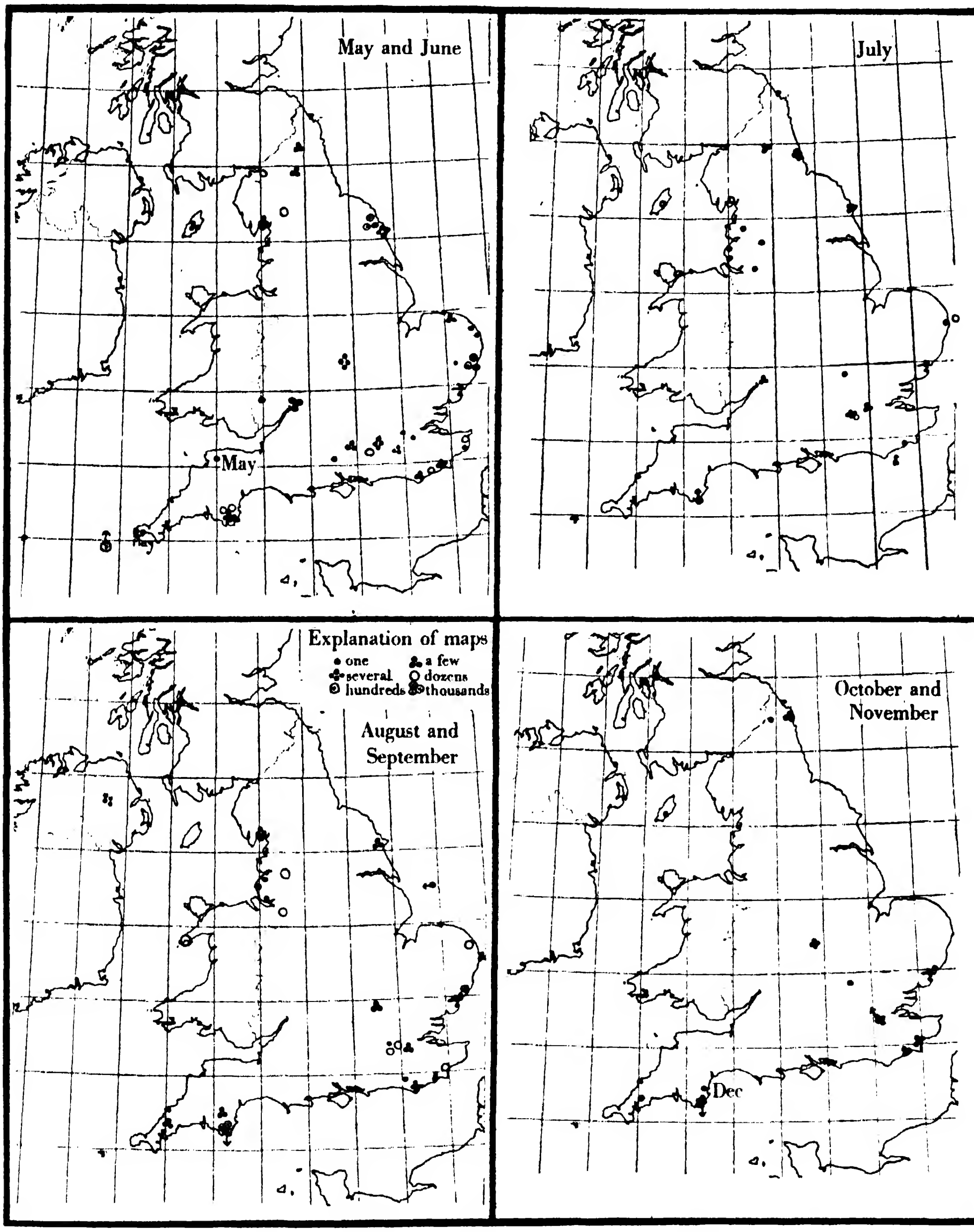


Fig. 2. Distribution of *Plusia gamma* in 1934.

was Annan in Dumfriesshire but, as in the previous year, this may have been due rather to a lack of observers further north than to actual absence of the species. Only a few scattered individuals were seen in September, and the last moth was seen in Devon on 23 October, the earliest last date that has been

recorded since the work began. Only two directional movements were recorded; six moths were observed from the East Dudgeon Light Vessel (24 miles out to sea, north of Hunstanton, Norfolk) while making their way westwards on 7 July; fourteen more, also flying towards the west, were seen in Barrow-on-Soar on 11 September.

1934. Records of *P. gamma* were far more numerous in 1934 than in previous years. This may have been partly due to the greater number of observers taking an interest in migration, but the fact that individual observers saw more moths at a time than they had in previous years shows that the species itself was more common. The season was a late one as a whole. The earliest arrival was seen on 28 May, and the main body of immigrants reached England at the beginning of the last week in June, when the species became very common in many places in the south, and was reported singly as far north as Unst in the Shetland Isles. (These last records are not shown in Fig. 2.) About this time a large immigration seems to have reached the extreme west of England from the south, perhaps from Spain via the Bay of Biscay. They were first observed in the Scillies, where dozens of them were seen flying north in the late afternoon of 22 June by Mr R. Trotter of the Round Island Lighthouse. Three days later they were seen in hundreds in several places in Gloucestershire and on the Welsh Borders; by 1 July they had disappeared from these localities, and further evidence of their movements is lacking. From Devon to east Kent the species was numerous by the end of June, and oviposition was reported from Dartmoor on 27 June.

Immigration from the south continued very late in 1934, since moths were seen coming in from the sea in south Devon on 21 July, and in the Channel near Folkestone on the following day. Only one moth was seen flying westwards in August; but as that was observed 30 miles out to sea off the east coast (Outer Dowsing Light Vessel), even by itself it is a faint indication of migration in this direction. On 12 September Mr A. W. Godfrey, of the Start Lighthouse, near Hallsands in south Devon, saw a large migration going out to sea southward between 9 and 11.30 p.m. Many of the moths were attracted to the light and rested on the glass of the lantern, so he was able to secure a number of specimens for identification. This experience of southward migration was repeated on 23 September and 2 October at the same place, but on these occasions the numbers were much smaller.

The moths continued to increase in number until mid-September, although they were never so common as they had been in spring. At the end of the month they began to decrease rapidly; only two individuals were seen after the third week in October, but one of these was exceptionally late (3 December). No more moths were seen from then until the following May.

1935. Much more regular observations were made in 1935 than in previous years, especially in Hastings, where Mr H. G. Macleod took nightly counts throughout the summer. These observations, which are most valuable, have

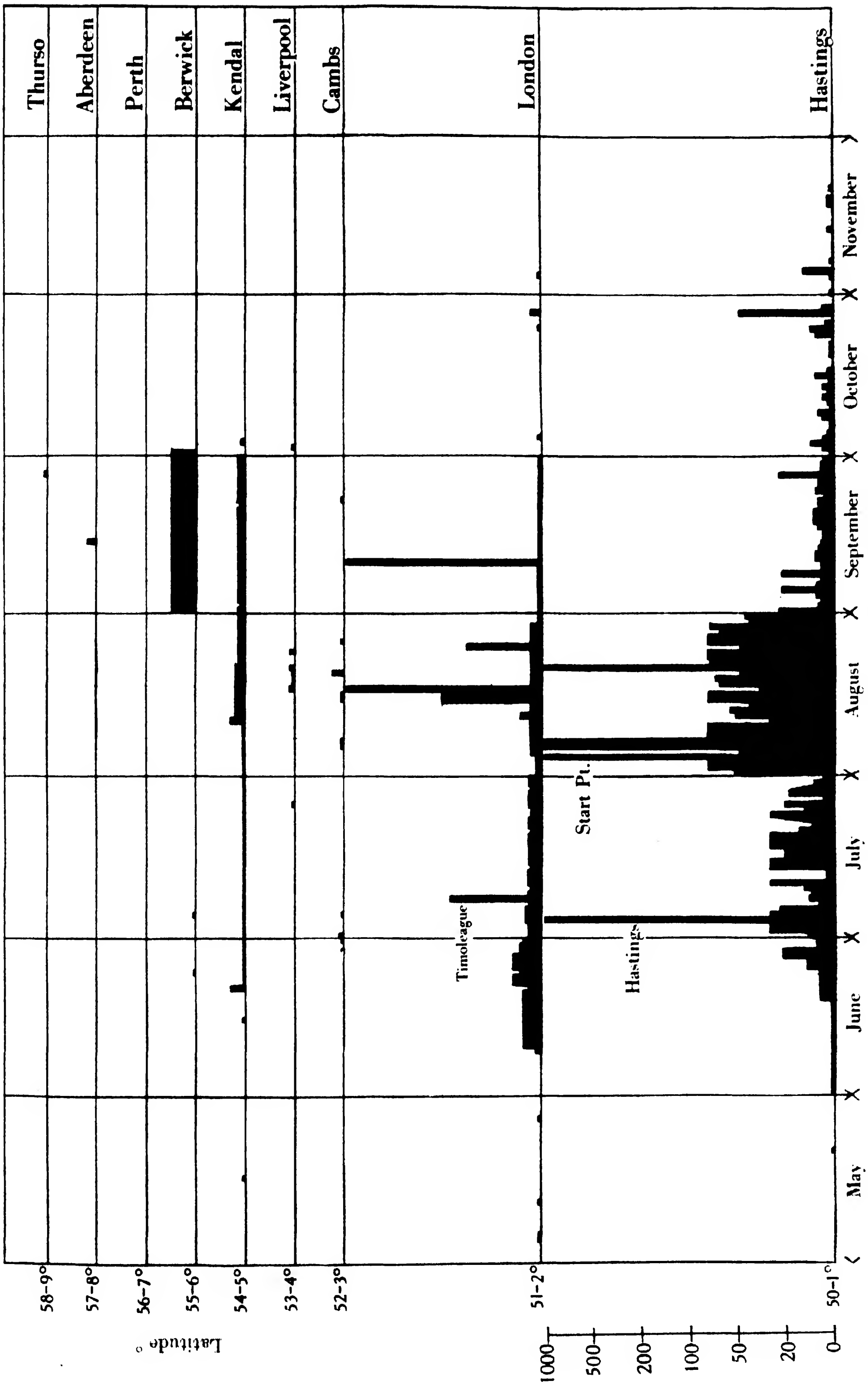


Fig. 3. Distribution of *Plusia gamma* n 1935.
(Vertical scale = av. no. seen per observer per day.)

been continued ever since. The form of graph used in Figs. 3 and 6 to illustrate the distribution in this year and in 1936 needs some explanation. The graph is

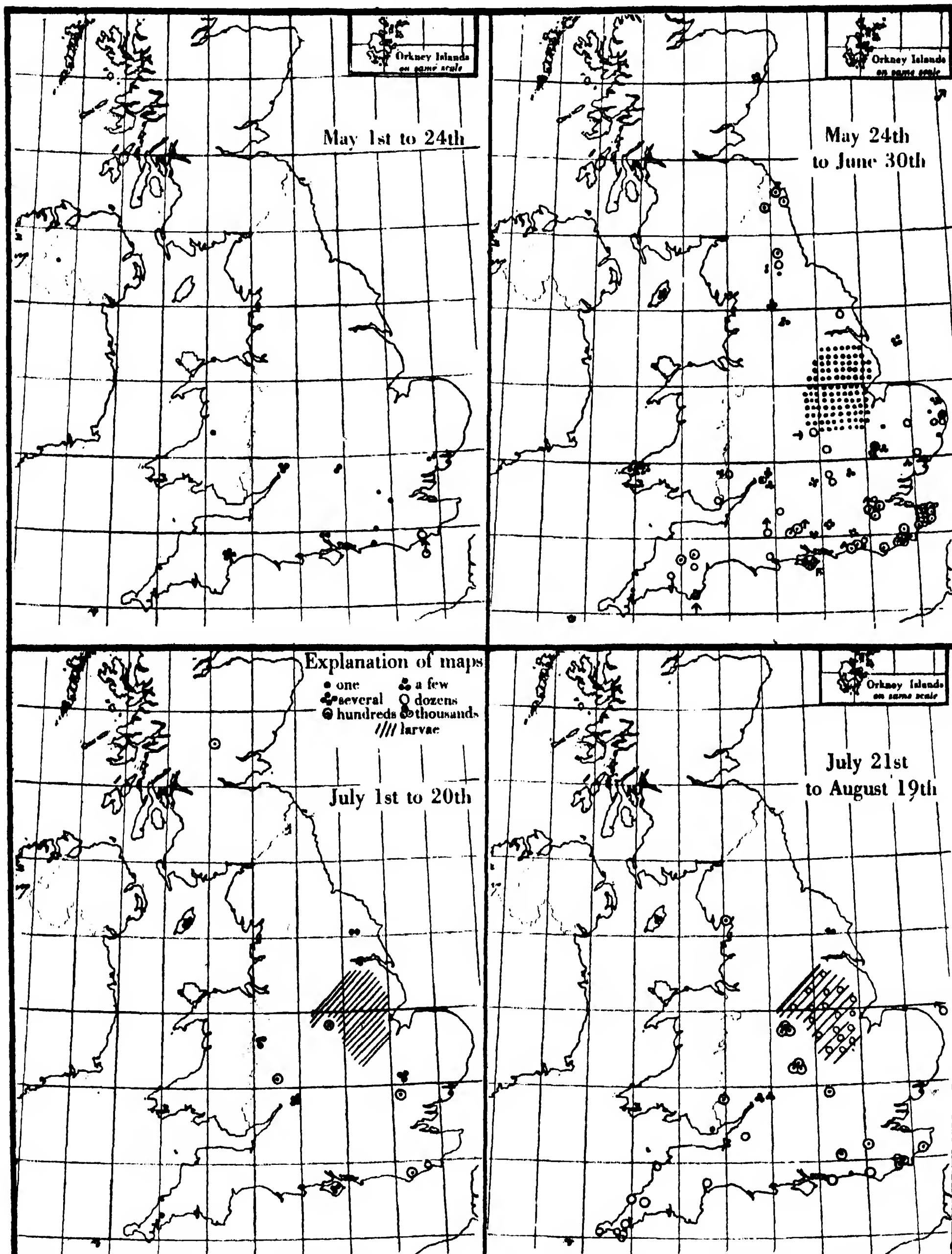


Fig. 4. Distribution of *Plusia gamma* in 1936.

divided into horizontal strips, each one of which represents a degree of latitude. In the 1935 graph, the lower strips are wider than the others, to accommodate the greater number of insects recorded from the southern counties; the vertical

scale of abundance is the same. The vertical column represents the average number of insects seen per observer each day. Since the number of observers

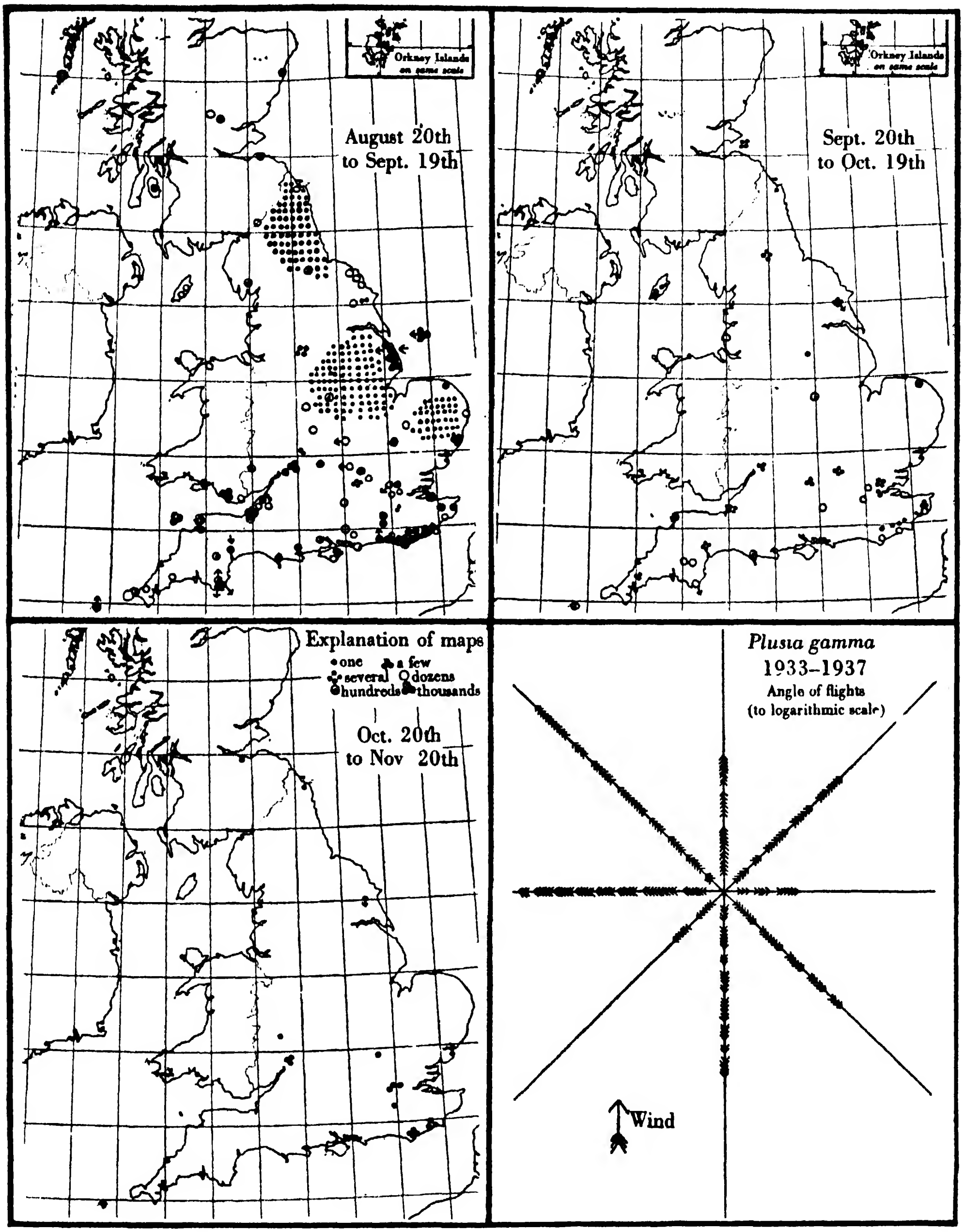


Fig. 5. Distribution of *Plusia gamma* in 1936.

decreases rapidly towards the north, a direct addition of all moths recorded per day in each degree would result in an exaggeration of the numbers seen in the south; this error is largely obviated by averaging the number per observer.

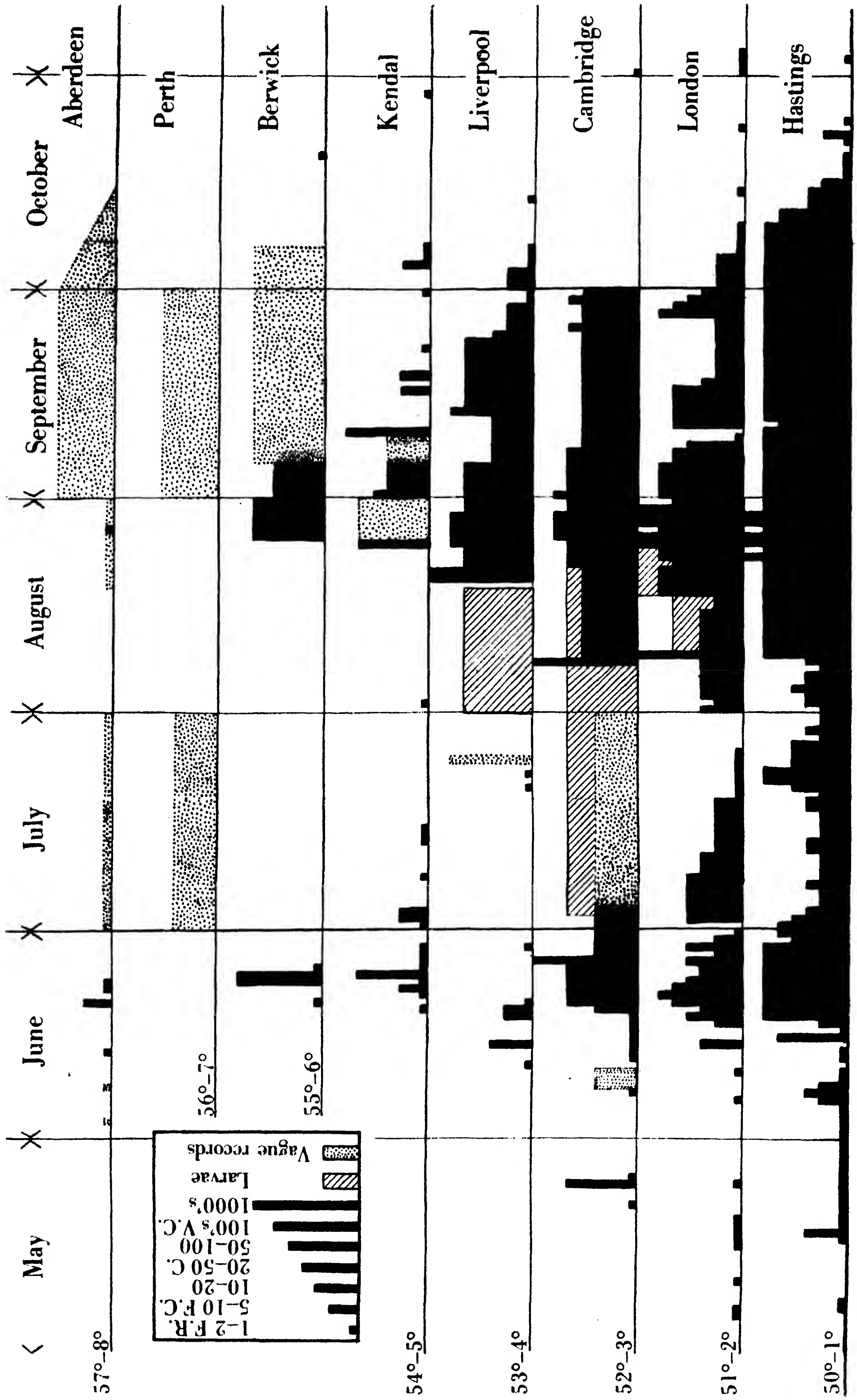


Fig. 6. Distribution of *Plusia gamma* in 1936.

The number seen in the south is still greater than in the north, but this is a real effect and does not depend on the number of observers.

The first moth seen in 1935 was recorded in Timoleague (Ireland) on 5 May. Maximum summer emergences also took place earlier than in 1934, quite large numbers being counted in August; a large southward migration from the Start was witnessed on the 4th of that month. The moths had a considerable northward range, being reported from the extreme north of Scotland; but on the whole they were uncommon except in the south. In one or two places they appeared in large numbers, but as this was only for one or two days at a time, it is probable that these were migrations passing through. A few solitary moths were again seen flying westwards in August from the Outer Dowsing Light Vessel (30 miles to the east of Spurn Head), in this case after the southward emigration of British bred moths had begun. Numbers decreased very suddenly at the beginning of September over most of the country, though it appears as if an emergence had taken place in southern Scotland about this time. A few moths lingered on until the beginning of November and one solitary individual was seen in Hastings on the 21st of that month.

1936. This was perhaps the most remarkable *P. gamma* year ever fully recorded. The species was extremely common and widespread, and was seen as far north as Fair Isle (Shetland). In some parts of southern England the moths were so numerous that observers gave up attempting to estimate their numbers in thousands and reported them in "myriads". A curious feature of the summer distribution, noticeable in other years, but emphasized in this year of plenty, is the great variation in numbers between neighbourhoods quite close to one another. This may perhaps be attributable to gregariousness, since the migrations of *P. gamma* frequently seem to include much greater numbers of individuals than do flights of most of the other regular migrants in this country. Harpenden, in Hertfordshire, seems to be one of the places where the species is regularly less common than elsewhere. Here at Rothamsted a light trap has been run nightly over the greater part of the period dealt with in this paper, and personal observations have also been made during daylight. Yet, in 1935, at a time when a light trap only a few miles away on the Buckinghamshire-Bedfordshire border was catching as many as 400 *P. gamma* in one night, only solitary individuals were seen in Harpenden, and in 1936, when the moths were reported in thousands all over the country, the largest count made near Harpenden was a little over a hundred, and that only on one day and after considerable search.

1936 was a fairly early year. The first migrant was seen in Croydon on 6 May, and immigrants were seen flying northwards in late May and June. During the latter month swarms of moths reached the sugar-beet fields of Lincolnshire and Norfolk in such numbers that the sound of their wings was audible as a distinct humming, and the crops were damaged later by the resulting larvae. Extensive breeding also probably took place in northern

Europe, since flights westwards across the North Sea reached enormous proportions in August. During the first three weeks of August these westerly movements predominated; from the end of that month until October flight direction was chiefly towards the south. There was a certain amount of overlap between these two flight directions, however, and the position was further complicated by several definite immigrations of quite large numbers of the moths from the south. During October the number of moths present in Great Britain decreased fairly rapidly, but a few persisted until the end of that month, and occasional individuals were seen until the end of November.

1937. Up to the end of September very few records for this year have as yet come to hand. As far as can be ascertained, the moths have been definitely uncommon everywhere, both in spring and summer. Three southward migrations have, however, again been seen at the Start Lighthouse, all during August; two of these movements were comparatively thin, but one comprised some thousands of moths.

3. Seasonal variation of flight direction

Fig. 7 is intended to show how the direction of flight in *P. gamma* varies during the summer, and was made by combining all the flights in which direction was recorded from 1933 to 1937 (no directional flights were reported in 1932). Each separate flight is represented by a group of darts pointing in the appropriate compass direction, and even single individuals have been included. The flights vary greatly in number, from one to many thousands, and for convenience in representation a logarithmic scale has been used. Thus,

1	dart represents	1	moth
2	darts represent	2	moths
3	,,	5	,,
4	,,	10	,,
5	,,	21	,,
6	,,	46	,,
7	,,	100	,,
8	,,	210	,,
9	,,	460	,,
10	,,	1000	,,

and so on, so that a large number of small flights tends to show a similar importance to a small number of large flights. This is designed to effect a compromise between putting in a dart for each insect, which is impossible for reasons of space, and putting in a dart for each flight, which would altogether exaggerate the importance of solitary insects which may or may not have been migrating when recorded.

It will be seen from the summary of records for the past five years that solitary moths begin to appear in May, after an absence of five months. They

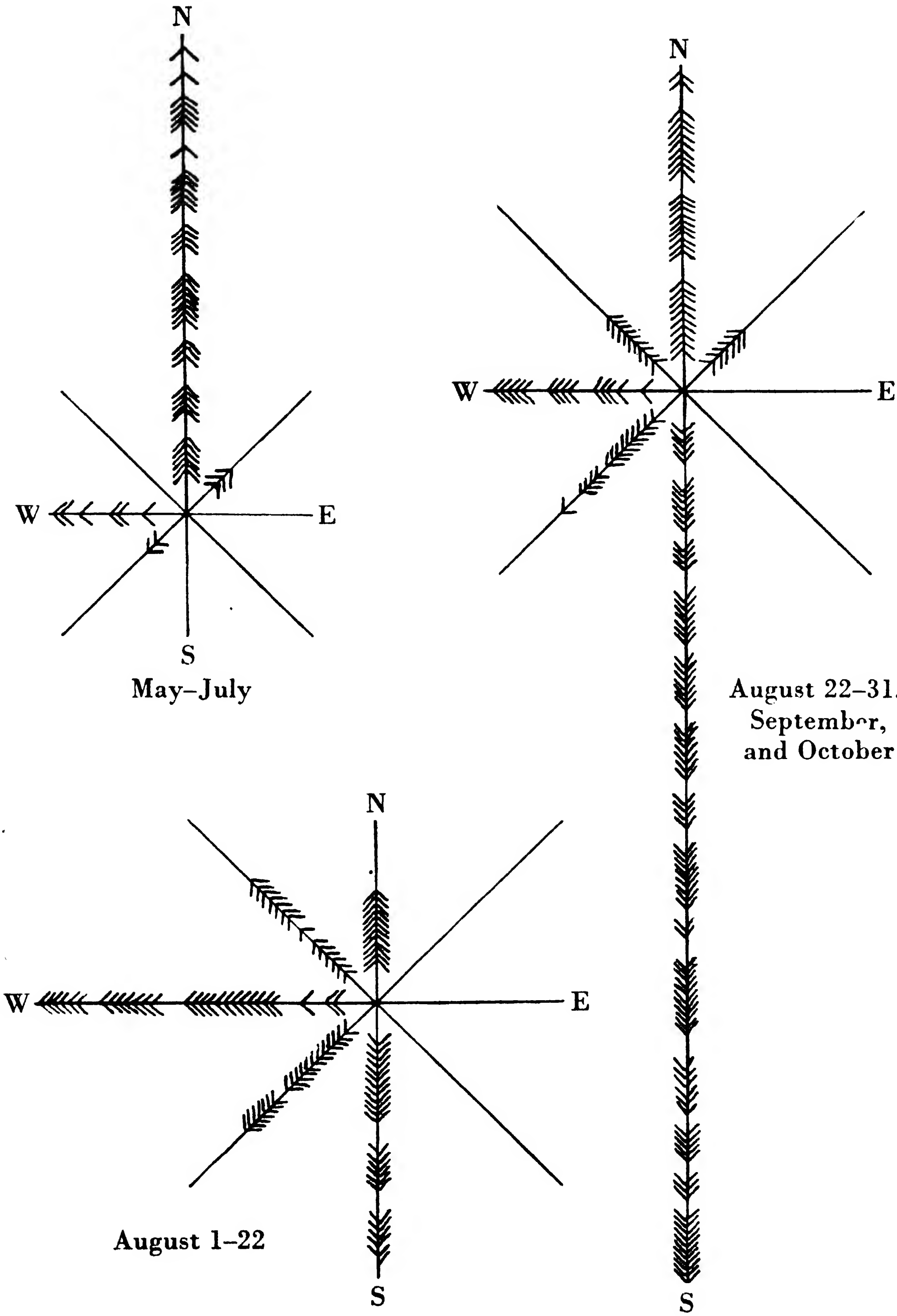


Fig. 7. Directional flights of *Plusia gamma* from 1933 to 1936, with a few flights of 1937.

are followed by gradually increasing numbers through May and June, the maximum number of immigrants being reached five or six weeks after the first appearance. During this period the direction of flight is predominantly northwards. In July, although some immigration may occur, the majority of the moths lay their eggs and die, and the number of adult moths seen is considerably reduced (Figs. 3 and 6). The emergence of the adult generation usually occurs in August, though it may begin as early as July, or be retarded until September. There seems to be some connexion between the time of arrival of the first immigrants and the time of emergence of the British bred moths: if the first is delayed, the latter is late also. In four years out of five, westerly migrations have been observed, the moths entering Great Britain across the North Sea from some unknown point further east. This westerly movement is preponderant in early August, though it may occur as early as June or as late as September.

The moths which emerge in summer commence to feed upon the nectar of flowers, and being active by day as well as by night, may be observed to fly and to feed greedily in bright sunshine. Such females as have been dissected in autumn have their ovaries small and eggs undeveloped, and both sexes have copious fat bodies. From late August onward flight direction is preponderantly south, though there may be overlapping of westerly and southerly flights. In an unusually early year, large numbers may emigrate in the beginning of August, as in 1935. Immigrations from the south may take place in late August, at the same time that British bred moths are moving in the opposite direction; these flights, however, are probably to be regarded as exceptional.

4. General factors influencing migration

The actual commencement of a migratory flight of *P. gamma* has twice been witnessed in this country, once by the late Robert Adkin on the Downs behind Walmer in Kent, and once by Mr L. W. Newman (*in litt.*), at the foot of the hills near Folkestone. Mr Newman saw the moths rise from a field at dusk in a spiral and make for the sea; the time was late September. Adkin (1920) also saw the moths fly upward from a field in the evening; but in this case, although great numbers were seen to rise from the corn, they flew so high that they went out of sight and it was impossible to distinguish the direction in which they eventually flew. The evening was warm and calm and it was still light.

If the place and time of commencement of all observed migrations were known, very interesting correlations with weather conditions might be made. In the absence of direct evidence, however, it is possible to trace lines back across the map in the direction from which flights have come, and to select the most likely points on these lines for their possible origins (i.e. in the case of immigrants, the nearest point across the Channel). Weather records for the selected areas can then be obtained, and correlation attempted. If the results

Table 1

Observations of flight in progress				Conditions at possible starting place of migration				
Date	Place	No. of insects	Direction of flight	Date	Place	Barometer	Thermometer	Wind
1933								
7 June	East Dudgeon Lightship	6	W.S.W.	4–6 June	North Friesland	Falling to 6th, rising	Variable	S.E. then N.E., gentle
1934								
22 June	Round Island Lighthouse, Scilly	Dozens	N.	19–21 June	North-west Spain	Falling slowly	Slight rise	Calm
12 Sept.	Start Lighthouse, South Devon	Very large numbers	S. out to sea	10–12 Sept.	South Devon	Rising slowly	Rising slowly	Mainly light S. or S.W.
1936								
18 May	Hastings	Over 50	N. in from sea	15–18 May	Dieppe district	Falling 15–16, rising 17–18	Rising, then steady	Light variable
8 Aug.	Haisbro' Lightship	Dozens	N.W.	5–8 Aug.	Zeeland	Rising generally	Slight rise on 7th	Moderate S.W., veering N.E.
20 Aug.	Outer Dowsing Lightship	Many thousands	W.	17–19 Aug.	East Friesland	Falling a little on 19th	Falling	S.E. or S. light airs
24–30 Aug.	Exmouth	Hundreds	S.	22–28 Aug.	South Devon	Rising	Rising or steady	N. or N.W. fresh, falling calm

are at all regular and seem to show some connexion between migrations and weather factors, we may consider our original assumption as to starting points of the flights to be justified.

About fifty flights recorded under the Insect Immigration Scheme have been examined in this way, and the Meteorological Office have been kind enough to supply relevant weather records for the three days preceding each flight. Since the actual time of departure is unknown, there is no advantage in obtaining the exact figures for temperature and pressure; attention has only been given to whether the thermometer and barometer were rising, falling, or remaining steady during the period preceding the flights. Flights containing only one or two individuals have been neglected. Table 1 illustrates the way in which the available evidence has been gathered together: the first four columns show some of the particulars observed while the flights were in progress, while the remaining five columns show the conditions which prevailed in the Continental districts chosen. Where considerable fluctuations of pressure or temperature occurred, the conditions of the last day before the flight have been used in making the tables.

Tables 2 and 3 give the results so far obtained for pressure and temperature for most of the flights examined; they are divided into three parts according to the direction of the flights when observed. (No easterly flights were recorded.) Where flights were recorded as south-west or north-west one half has been credited to each direction. Tables 6 and 7, in the next section, show wind speed and direction at starting points.

Table 2. *Barometric pressure at supposed origin of flights*, 1933–6

Barometer	... ...	Rising	Falling	Little change
Flight direction	North	14	10	1½
	West	8	1	1½
	South	11	1	3
	Total	33	12	6

Table 3. *Temperature at supposed origin of flights*

Thermometer	... ...	Rising	Falling	Little change
Flight direction	North	8½	3	13
	West	4	3	3½
	South	8½	1	3½
	Total	21	7	20

Taken together, these tables seem to show a distinct tendency for flights to occur during or after periods of light to moderate winds, with rising barometer and rising or steady temperature. Such conditions are usually associated with anticyclonic weather; they are most favourable for crossing the sea, and are likely to improve rather than to deteriorate.

Although reached by a process not far removed from guesswork, the results are consistent enough to suggest that they are not far wide of the truth. It will be noticed that the effect of weather conditions is most strongly marked in the case of the southerly flights. This is to be expected, since there is much less doubt of the starting points in these cases; most of the southerly flights probably started quite close to the places where they were observed, while many of the northerly flights may have originated in districts far inland from the nearest points across the Channel which were used as a basis for the tables.

5. The effect of wind on migration

It has often been supposed that all the so-called migrations of Lepidoptera are involuntary, and that they are due to the insects being helplessly blown along by the wind. If this were so, we should expect migrations to occur in more boisterous conditions than those described above, and in particular to take place in periods of strong winds rather than in calms. We should also expect the direction of flight always to agree with that of the wind, both at the starting point of the migration and wherever the flights were later observed.

In many of the available records, not only is the direction of the wind at the time of observation recorded, but also its strength in Beaufort numbers or their equivalent. These numbers were devised by Admiral Beaufort to allow winds to be divided into classes according to strength estimated by various means, and are used by sailors and meteorologists. The numbers are placed in the first row of the following tables, and their equivalent in miles per hour is recorded beneath each one. Table 4 shows the various strengths of winds in which migrations in different directions have been seen passing; Table 5 gives the same data, but shows whether the flight was in each case with, against, or across the wind. The column corresponding to Force 0, or Calm, has been left out of the second table as it is of course impossible to say that moths fly with or against a calm. Another discrepancy between the two tables is accounted for by the fact that some records state that flights took place in winds of variable direction, giving the strength but not the compass points; these could be included in the first table but not in the second. They are well worth notice, since the fact that a flight has taken place in a wind of, say, Force 3, which varied in direction without affecting the direction of the flight, is in itself a repudiation of the theory that migration is wholly due to the action of wind.

One of the most remarkable records of this kind reports a migration of hundreds of *P. gamma* to the north in the Scilly Isles in 1936. The flight continued for eight days, although the wind blew sometimes against the line of flight and sometimes across it, and varied in strength from a light breeze to Force 5 (19–24 m.p.h.) or even higher. It is unlikely, however, that the moths allowed themselves to be exposed to the full force of this wind for more than a few seconds at a time; observations made on other occasions show that when

these and other Lepidoptera are flying in a strong wind they tend to keep low among the herbage, and to take advantage of any cover they can find.

When flights are described as taking place partly with and partly across the wind (i.e. a flight to the north in a south-west wind), one half has been credited to each column. This has also been done when the strength of the wind is given as between two Beaufort numbers, for example, "Wind S. Force 2–3". It has sometimes been necessary to divide a flight into quarters on the same principle.

Table 4. *Wind force at place of observation of flights*, 1933–7

Beaufort numbers		0	1	2	3	4	5
= miles per hour	...	Calm	1–3	4–7	8–12	13–18	19–24
Flight direction	North	6½	3½	6½	5	1½	2
	West	1	3	4	1	.	.
	South	2	8	3	2	½	½
	Total	9½	14½	13½	8	2	2½

Table 5. *Relationship between flight and wind direction at various wind speeds, at place of observation*, 1933–7

Beaufort numbers	1	2	3	4	5	
= miles per hour ...	1–3	4–7	8–12	13–18	19–24	Total
Flight with wind	4	3	2½	.	.	9½
Flight against wind	4	4	3½	½	.	12
Flight across wind	5½	6½	2	1½	2½	18

Table 4 shows that, although flights are more numerous in light winds, nearly a quarter of the flights were observed in winds of Force 3 or over, and that more than one flight occurred in a wind of Force 5, i.e. a "Fresh Breeze", 19–24 miles per hour. Should wind be the important factor in migration, then flights at the higher speeds should be with the wind; flights against the wind, if they took place at all, should occur only in the gentle winds. Table 5 shows that this is not the case and that there are actually more flights against the wind than with it. The largest number of flights are those across the wind; this is natural, since two directions are included in the expression "across". If this figure is divided into two, to allow for this, it will be seen that there is practically no effect of wind at all; the preponderance of flights against, over flights with the wind is so small as not to be significant. The lower right-hand diagram on Fig. 5 illustrates the effect of wind in diagrammatic form. Here, all winds are reduced to one direction, and the angle of flight to that direction is calculated. No allowance is made for wind speed, but by arranging darts on the logarithmic system used in Fig. 7 some indication of the numbers of insects involved is given, as apart from the number of flights.

Tables 6 and 7 give the data for presumed starting points of the migrations, and the results are comparable to those shown in Tables 4 and 5. There is a tendency for the wind to be stronger at the presumed starting point than at the place of observation, and for more flights to be across the wind than with or against it, but the differences are small, and probably not significant.

Table 6. *Wind force at presumed starting place of flights*, 1933–6

Beaufort numbers = miles per hour ...	0 Calm	1 1–3	2 4–7	3 8–12	4 13–18	5 19–24
North	6	3	6	5	2½	3
West	.	1½	3	5	½	.
South	3½	4	3	2	1	2
Total	9½	8½	12	12	4	5

Table 7. *Relationship between flight and wind direction at various wind speeds, at presumed starting place*, 1933–6

Beaufort numbers = miles per hour ...	1 1–3	2 4–7	3 8–12	4 13–18	5 19–24	Total
Flight with wind	2	2	2¼	½	½	7¼
Flight against wind	1½	2¼	3	1	¾	8½
Flight across wind	4½	6¾	6¾	2½	3½	24

6. Summary

1. Records of the presence and movements in Great Britain of the moth *Plusia gamma* L. from 1932 to 1937 have been collected from amateur Lepidopterists and others by the Insect Immigration Committee of the South-Eastern Union of Scientific Societies. The moths have been seen in varying numbers in each of these years, and an account of their distribution in each year is given. Only two winter records have been received, although such records were specially asked for. Both these concerned pupae.

2. About fifty records give the direction of flight of the moths. From these it is shown that there is a general tendency for northward movements to preponderate in spring, and southward movements in autumn. Westward immigration from across the North Sea seems to occur regularly in mid-August.

3. A study of records in which direction and strength of wind are given show that wind direction has little or no effect on the direction of migratory flights, and that migrations can take place in adverse winds of Force 4 (13–18 m.p.h.) or in cross winds of Force 5 (19–24 m.p.h.).

4. Possible starting points of migrations have been chosen by prolonging the line of flight backwards from the point of observation to the nearest point on the Continent, and weather conditions for the period immediately preceding the flights have been studied. There appears to be a tendency for migrations to begin in periods of rising barometer, rising or steady temperature, and light or moderate winds. Wind direction at presumed starting points seems to have no influence on the direction of migration.

References

1. **Williams, C. B. (1930).** "The migration of butterflies." Edinburgh.
2. **Grant, K. J. (1937).** "An historical study of the migrations of *Celerio lineata lineata* Fab. and *Celerio lineata livornica* Esp. (Lepidoptera)." Trans. R. Ent. Soc. Lond. 86: 345–57.
3. **Adkin, R. (1920).** "Migrations of Lepidoptera in regard to the British Islands." S.-East. Nat. 25: 41–8.

BIRD AND ANIMAL ACTIVITY IN THE ARCTIC

By A. J. MARSHALL

In the past, almost without exception, zoologists have reported constant activity among birds and other animals in the perpetual light of the arctic summer. This is possibly accounted for by the extreme vigilance of all tundra species, coupled with the open nature of the country which renders the human observer visible at great distances. These arctic animals, naturally, are exceptionally alert, because of the open nature of their habitat. They have usually vacated their nesting or resting places and are very active indeed long before they are seen by the observer.

During a recent summer expedition to West Spitsbergen (Svalbard) attention was paid to the question of perpetual activity. Certain species of birds, notably the tern (*Sterna macrura*), the eider duck (*Somateria mollissima*), the skua (*Stercorarius parasiticus*) and possibly the purple sandpiper (*Calidris maritima*) undergo a distinct period of quiescence. At Klaas Billen Bay, in the "Inner Fjord Zone" (Summerhayes, V. S. & Elton, C. S. (1928), *J. Ecol.* 16: 256) this period appeared to extend for a couple of hours after 1 a.m. each day. It coincides roughly with the time during which the sunlight, temperature, and wind velocity are at a minimum. (For this information I am indebted to Prof. H. Tollner of the Zentralanstalt für Meteorologie, Vienna, a co-worker on our expedition.)

On one species only could satisfactory observation be made. This was the arctic tern, which had established an extensive ternery on the shingle about the huts in which we lived. These birds were in residence before we arrived, and after the first few hours we were subjected to a vicious attack by them every time we left the huts. They unmercifully persecuted the fulmar petrels and gulls which flew over the ternery from time to time, and no robbing skua dared approach their colony. During the quiescent period however, when the sitting tern slept on the eggs and its mate fitfully dozed a few yards away, passing kittiwakes (*Rissa tridactyla*) and fulmars (*Fulmarus glacialis*) and even the hereditary enemy the skua were allowed to fly over low without molestation. Despite the fact that the sitting bird was sleeping, the non-sitting bird never slept for more than a few minutes at a time. Time and again it would suddenly untuck its head and gaze suspiciously around, often making a short flight as if to satisfy itself that all was well. A human figure appearing half a mile away over the barren tundra would provoke the whole colony into noisy

activity. Had hiding facilities within the ternery not been available I would never have guessed that a period of comparative inactivity existed. And it is probable that a similar period occurs with many other species as well.

In the recently described glacial feeding zone (Hartley, C. H. & Fisher, J. (1936), *J. Anim. Ecol.* 5: 370) at the head of Klaas Billen Bay, there appeared to be, as Hartley and Fisher suggest, little evidence of any great numerical fluctuation in the constant stream of kittiwakes which flew to and fro along the coast and over the tundra. A few kittiwakes would doze after feeding, basking in the sunlight on the ice-smoothed boulders carried down to the bay by the nearby glacier. The vast majority, however, would return down fjord to their colonies. Contrary to Fisher and Hartley, we found (in 1937) fulmars far more numerous than kittiwakes in the feeding zone. For 24 hr. the fulmar flock fed with the kittiwakes at the mouths of the ice streams which poured from under the ice cliffs at the face of the glacier; individuals gradually falling away from the whirling, dipping mass to rest replete, dozing and preening on the water among the drifting ice-blocks. At about 6 a.m. the resting fulmar flock appeared to decrease in numbers, and during the day there were never so many birds resting on the water as during the "night" hours after 9 or 10 p.m. The birds were breeding in cliffs a couple of miles away. The stomachs of both species contained a great number of crustaceans.

In many other species I could detect no distinct rest period whatever. In the colonial cliff nesting species of little auks (*Alle alle*), puffins (*Fratercula arctica*) and guillemots (*Uria lomvia*) which we observed at Sudgat in the north-west of the island, I could find no slack period in either flight or fishing. For the whole of 24 hr. birds flew around the cliffs in great flocks, or otherwise exhibited constant activity: feeding, fishing or engaging in the curious noisy communal gatherings which one sometimes observes on the feeding waters. (Little auk: Montague, F. A. (1926), *Ibis*: 151; guillemot: Longstaff, T. G. (1924), *Ibis*: 493.)

At all times it was strikingly apparent that local weather conditions are a big factor in controlling activity. Unusually heavy winds, strong sunlight (and the rare period of excessive rain) always modified activity. The icy glacial winds sweeping over the tundra would force birds to take advantage of any scanty cover offered. A fine burst of sun would interrupt their feeding; and sandpipers, terns, gulls, snow-buntings and other birds perching fluffed in the pale sunlight would not be an unfamiliar sight.

Among the few mammals observed, the arctic fox (*Alopex lagopus*) and the ring seal (*Phoca hispida*) were noted at all times: the fox out foraging, the seal swimming, or basking on the floating bergs. I was unable to arrive at any definite conclusion about the activity of these mammals.

Summary

1. The arctic tern (*Sterna macrura*) and possibly other species, have periods of quiescence in the perpetual arctic light; and these periods may be correlated with meteorological conditions.

2. In many species, such as the fulmar petrel (*Fulmarus glacialis*), there is no apparent period of inactivity: it is possible that these rest only when replete or tired.

3. Local weather conditions (such as sudden sunlight or icy winds) may abruptly provoke inactivity.

THE FOOD OF PARTRIDGE CHICKS (*PERDIX PERDIX*) IN GREAT BRITAIN

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(*With 2 Figures in the Text*)

1. Introduction

THE work on which this paper is based forms part of a research into the ecology of game birds carried on by the Bureau of Animal Population. This research has been financed by a grant from Imperial Chemical Industries and by the donations of landowners and shooting men. We wish to thank all those who have helped in this way, and also by sending us specimens for examination.

We are indebted to E. Arthurs, Department of Botany, Oxford, for identification of some of the seeds; to E. W. Aubrook, Hope Department of Entomology, Oxford, who identified the Coleoptera; and to Dr K. G. Blair of the British Museum (Natural History) for a note on the *Phytonomus* larvae. We have also to thank Prof. G. D. Hale Carpenter who allowed us the facilities of the Hope Department of Entomology at Oxford for the entomological work.

2. Material and technique

The crop contents of sixty-nine partridge chicks, received between 1934 and 1937 from various estates in Britain, have been analysed. As it is extremely difficult to obtain young partridges for crop examination, our only source of material was through accidental deaths. Actually, the majority of the birds we examined were killed by mowing machines cutting hay, clover, lucerne, etc., in which the young birds were living. Our sample is not, therefore, truly representative of the whole population. Probably more young partridges live in growing corn crops than in grass and clover, but there was no means of obtaining specimens from corn crops in June and July, during the first 6 weeks of the partridge's life. This fact naturally limits the invertebrate fauna available to the birds we examined, especially those under about 2 weeks of age. The older chicks, being able to fly from one field to another, probably took a more random sample of the food available in both green and corn crops.

The contents of each crop, mainly insect material, were stored in alcohol until time for sorting. The process of sorting was as follows. All vegetable

material was separated out and treated as described in a previous paper (**1**). The insects and other animals were then sorted into orders and kept in separate tubes of alcohol, except for the beetles and some bugs which were dried and mounted for identification. The numbers of individuals of each species or group of species were recorded on separate cards for each crop. These cards are preserved in the Bureau of Animal Population.

Before determining the volumes of the various constituents, the crops were arranged in four age classes: from hatching until 7 days, from 8 to 14, from 15 to 21 and over 21 days. When the age of a chick was not known from the

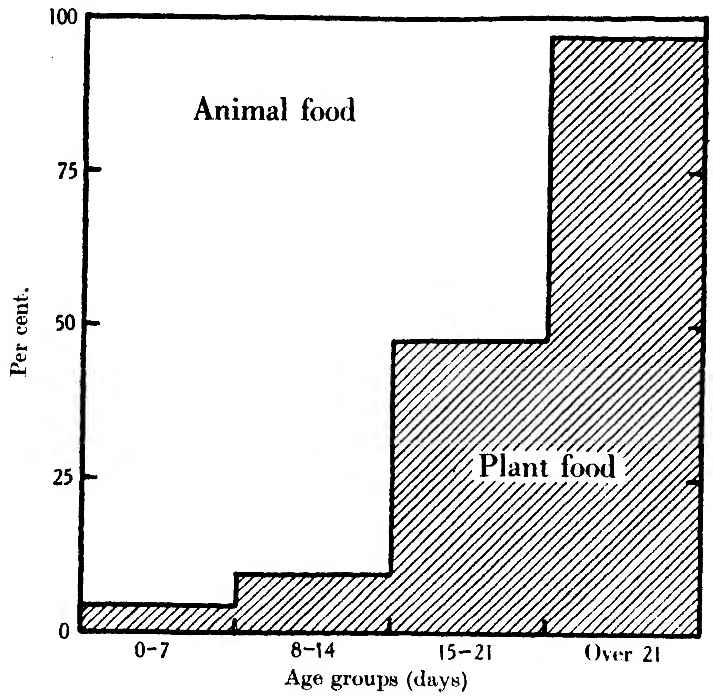

Fig. 1. Proportions by volume of animal and plant foods in partridge chick crops.

original data, this was estimated from its weight by use of the weight/age curve shown in Fig. 2. This curve has been compiled from data obtained from hand-reared chicks of known age (Table 1).

In the determination of volumes, insects, etc., of the same species, or group of species, were combined in each age class; excess alcohol was removed with blotting paper, and the volume determined by displacement in a measuring tube containing alcohol. Species which had been dried for identification were first boiled for 5 min. to expel enclosed air and remove them from the mounting cards; the water was then poured off and they were washed with cold alcohol. They were then measured volumetrically as above. The boiling treatment is necessary, as without it the dried insects will float in the measuring tube.

Table 1. *Weights of partridges at different ages*

Age in days	Average weights in grams of four groups of partridges reared (*a*)	(*b*)	(*c*)	(*d*)
1	10·0	—	—	—
2	9·3	—	—	—
3	9·1	—	—	—
4	10·6	—	—	—
5	12·1	—	—	—
6	12·9	14·9	—	—
7	—	—	18·8	18·4
8	16·4	—	—	—
9	18·5	—	—	—
11	23·0	—	—	—
12	25·4	—	—	—
13	27·3	28·0	—	—
14	28·3	—	27·0	35·4
15	32·2	—	—	—
16	33·1		—	—
17	35·1	—	—	—
18	38·8	—	—	—
19	40·3	—	—	—
20	41·5	44·5	—	—
22	46·1	—	43·5	—
23	50·7	—	—	—
27	—	68·0	—	—
28	—	—	68·5	—
34	—	94·5	—	—
35	—	—	101·4	—
42	—	—	130·3	—

3. RESULTS OF CROP ANALYSIS

(*a*) *Animal food.* Table 2 gives the species or groups of species of insects and other animals identified in all crops, together with the numbers of each obtained in each age class. Where a species occurred in more than one crop the frequency is given in brackets.

In many instances the specimens were too mangled for complete identification, especially Diptera and nymphs of Heteroptera. In some cases, especially the Aphididae, where the naming of species would have involved seeking the co-operation of specialists, we have been content with names of orders or families. The parasitic Hymenoptera, various arachnids and the larvae of Lepidoptera, which also were not fully identified, comprised a large number of species, no one of which had any importance numerically. Altogether 143 identifications are listed, though the actual total of species is probably in the neighbourhood of 200.

Tables 3–6 summarize the individual crop analyses in the four age classes. Each crop is given a reference number for the locality from which it was obtained. The following is a list of these localities, with the numbers pertaining to them:

HAMPSHIRE. Tichborne, 1, 2; Sutton Scotney, 19, 20, 21, 25, 26, 39, 53; Alresford, 41; Red Rice, 52; Lymington, 58. ISLE OF WIGHT. Bowcombe, 42, 50, 51. SUSSEX. Amberley, 22, 23. BERKSHIRE. Ilsley, 32, 33, 34, 46, 55;

Table 2. *Animal species identified, with abundance and frequency in each age class*

	1st week	2nd week	3rd week	Over 3 weeks	Total
INSECTA					
COLLEMBOLA					
Sminthurus viridis L.	556 (18)	611 (15)	64 (5)	—	1231
? *Orchesella* sp.	1	9 (3)	—	—	10
ORTHOPTERA					
Blattidae					
Ectobius panzeri Steph.	—	—	—	2	2
Acridiidae (spp. indet. nymphs)	7 (3)	18 (3)	1	1	27
DERMAPTERA					
Forficula auricularia L.	29 (6)	4 (2)	3 (3)	2	38
HEMIPTERA-HETEROPTERA					
Coreidae (sp. indet.)	—	4	—	—	4
Lygaeidae (spp. indet.)	1	—	11	—	12
Reduviidae					
Nabis sp.	—	4	1	—	5
Anthocoridae					
? *Anthocoris* sp.	—	—	2	—	2
Capsidae					
Lygus sp.	—	—	1	—	1
Spp. indet.	8	103 (4)	35	—	146
Other Heteroptera indet.	10 (4)	21 (3)	4	—	35
HEMIPTERA-HOMOPTERA					
Delphacidae					
Delphacinus mesomelas Boh.	1	—	—	—	1
? *Delphacinus* sp.	—	—	1	—	1
Cercopidae					
Philaenus spumarius L.	1	3 (2)	5	—	9
Philaenus campestris Fall.	—	4	—	—	4
Philaenus sp. nymphs	—	2 (2)	1	—	3
Jassidae					
Acocephalus albifrons L.	2	2	1	—	5
Acocephalus bifasciatus L.	—	1	—	—	1
Acocephalus nervosus Schrk.	—	—	1	—	1
Acocephalus spp. nymphs	28 (7)	23 (6)	57 (3)	1	109
Eupelix cuspidata Fab.	—	—	8	—	8
Athysanus obscurellus Kbm.	—	—	1	—	1
Athysanus sp.	—	—	2	—	2
Deltocephalus pascuellus Fall.	—	13	—	—	13
Deltocephalus ocellaris Fall.	—	—	5	—	5
Deltocephalus pulicaris Fall.	—	3 (3)	—	—	3
Deltocephalus socialis Flor.	4 (2)	4	2	—	10
Deltocephalus sp. nymphs	11 (4)	3 (2)	15 (4)	5	34
Limotettix 4-notata Fab.	5	9 (2)	—	—	14
Limotettix ? sulphurella Zett.	—	—	10	—	10
? *Limotettix* sp.	1	3 (2)	—	—	4
Cicadula sexnotata Fall.	4	1	—	—	5
Cicadula sp.	—	1	—	—	1
Spp. indet. nymphs	32 (7)	23 (8)	10 (3)	—	65
Aphididae (spp. indet.)	468 (17)	251 (11)	23 (3)	4 (2)	746
Aleyrodidae (spp. indet.)	—	8	45	—	53
NEUROPTERA					
Chrysopidae					
? *Chrysopa* sp.	—	—	—	1	1
LEPIDOPTERA					
Imagines, spp. indet.	3	10	19 (3)	1	33
Larvae, spp. indet.	60 (15)	24 (11)	17 (6)	2 (2)	103
COLEOPTERA					
Staphylinidae					
Tachyporus hypnorum F.	1	7 (3)	4 (3)	—	12
Tachyporus chrysomelinus L.	1	2 (2)	—	—	3
Tachyporus sp.	—	—	1	—	1
Tachinus sp.	—	1	—	—	1

Table 2 (*cont.*)

	1st week	2nd week	3rd week	Over 3 weeks	Total
COLEOPTERA (*cont.*)					
Staphylinidae					
Astilbus caniculatus F.	2	—	—	—	2
Xantholinus linearis Ol.	—	—	1	—	1
Philonthus varius Gyll.	—	2 (2)	—	—	2
Oxytelus sp.	—	1	—	—	1
Stenus similis Hbst.	—	—	2	—	2
Hypocyptus longicornis Pk.	—	1	—	—	1
Curculionidae (Weevils)					
Phyllobius viridiaeris Laich.	32 (3)	137 (2)	—	—	169
Phyllobius parvulus Ol.	—	2	—	—	2
Sitona sulcifrons Thunb.	1	1	3 (2)	—	5
Sitona humeralis Steph.	—	2	1	—	3
Sitona puncticollis Steph.	10 (4)	52 (5)	9 (2)	1	72
Sitona lineatus L.	1	—	1	—	2
Sitona hispidulus F.	—	7 (5)	—	—	7
Sitona flavescens Marsh.	—	1	—	—	1
Sitona crinitus Hbst.	—	—	—	1	1
Sitona sp.	1	1	—	1	3
Apion assimile Kirb.	5	1	4 (2)	—	10
Apion aestivum Germ.	1	—	9 (3)	—	10
Apion curtirostre Germ.	1	1	—	—	2
Apion flavipes Pk.	—	1	1	—	2
Apion pisi F.	—	—	—	2	2
Apion loti Kirb.	—	—	1	—	1
Apion apricans Hbst.	—	—	1	—	1
Apion sp.	1	2 (2)	—	—	3
Phytonomus nigrirostris F.	7 (3)	3 (3)	1	—	11
Phytonomus punctatus F.		1			1
Phytonomus trilineatus Marsh.	—	—	1		1
Phytonomus sp.	—	1	1	—	2
Phytonomus larvae	501 (14)	222 (9)	114 (4)		837
Miccotrogus picirostris F.	2 (2)	—	—	—	2
Rhinoncus pericarpius L.	—	—	1	—	1
Gymnetron sp.	—	—	1	—	1
Amalus haemorrhous Hbst.	—	—	—	1	1
Liosoma deflexum Pz.		1		—	1
Philopedon plagiatus Schol.	—	—	—	2	2
Stenocarus fuliginosus Marsh.	—	—		1	1
Carabidae					
Bembidion lampros Hbst.	1	1		—	2
Pterostichus madidus F.	—	—	1		1
Pterostichus sp.	—	—	1	—	1
Metabletus obscuroguttatus Duft.	—	—	1		1
Amara communis Pz.	—	—	1		1
Demetrius atricapillus L.	1	—	—	—	1
Trechus quadristriatus Schr.	—	7 (2)	—	—	7
Harpalus aeneus F.	—	—	—	1	1
Anchomenus dorsalis Pont.	—	—	—	1	1
Chrysomelidae					
Chaetocnema concinna Marsh.	—	—	—	2	2
Phyllotreta nodicornis Marsh.	—		—	1	1
Phyllotreta vittula Redt.	—	—	—	1	1
Crepidodera ferruginea Scop.	—	1	—	—	1
Longitarsus sp.	—	—	1	—	1
Cantharidae					
Cantharis fulvicollis F.	—	1	—	—	1
Cantharis lateralis L.	—	3	—	—	3
Malachius viridis F.	—	1	—	—	1
Elateridae					
Agriotes lineatus L.	—	2 (2)	2 (2)	—	4
Agriotes sputator L.	—	3 (3)	1	—	4
Agriotes obscurus L.	—	4 (3)	1	—	5
Athous longicollis Ol.	—	—	1	—	1
Adrastus nitidulus Marsh.	—	—	—	1	1
Byrrhidae					
Simplocaria semistriata Ill.	—	2	—	—	2

Table 2 (*cont.*)

	1st week	2nd week	3rd week	Over 3 weeks	Total
COLEOPTERA (*cont.*)					
Cholevidae					
Ptomophagus subvillosus Goez.	1	—	—	—	1
Lathridiidae					
Enicmus transversus Ol.	1	—	—	—	1
Coccinellidae					
Micraspis 16-punctata L.	—	—	1	—	1
Nitidulidae					
Meligethes viridescens F.	—	—	—	15	15
HYMENOPTERA					
Tenthredinoidea					
Cephus pygmaeus L.	1	—	—	—	1
Rhogogaster viridis L.	—	1	—	—	1
Ichneumonoidea (spp. indet.)	5 (3)	12 (3)	3 (3)	1	21
Proctotrypoidea (spp. indet.)	3 (3)	4 (2)	—	1	8
Chalcidoidea (spp. indet.)	6 (5)	3 (3)	1	—	10
Cynipoidea (sp. indet.)	1	—	—	—	1
Formicoidea (Ants)					
Myrmica scabrinodis Nyl.	—	8 (2)	—	—	8
Acanthomyops flavus F.	—	73 (4)	522 (3)	—	595
Acanthomyops niger L.	9 (4)	17 (5)	2	12 (4)	40
Cocoons	—	258 (3)	1625 (4)	—	1883
Larvae	—	23	—	—	23
Other Hymenoptera indet.	4 (3)	4 (3)	8 (5)	—	16
DIPTERA (Flies)					
Tipulidae					
Tipula spp.	2 (2)	1	—	—	3
Limnobius sp.	1	—	—	—	1
Asilidae					
Leptogaster cylindrica Deg.	—	1	—	—	1
Empidae					
Hilara sp.	—	1	—	—	1
Dolichopodidae (spp. indet.)	—	2	—	—	2
Phoridae (spp. indet.)	1	1	—	—	2
Pipunculidae					
Pipunculus sp.	—	1	—	—	1
Trypaneidae					
Ditricha guttularis Meig.	—	1	—	—	1
?Sapromyzidae (spp. indet.)	—	2 (2)	—	—	2
Agromyzidae (spp. indet.)	1	1	—	—	2
Ephydridae					
Hydrina sexmaculata Becker	—	1	—	—	1
Chloropidae					
Meromyza variegata Meig.	—	—	1	—	1
Meromyza sp.	1	4 (2)	1	—	6
Spp. indet.	5 (3)	6	4 (2)	5 (3)	20
Tachinidae (sp. indet.)	—	—	—	1	1
Muscidae (spp. indet.)	1	1	—	—	2
Other Diptera indet.	4 (3)	2 (2)	—	1	7
INSECTS INDETERMINABLE					
Imagines	11 (6)	1	—	3 (2)	15
Larvae	12 (7)	24 (9)	3 (2)	5 (5)	44
ARACHNIDA					
Acarina (Mites) (spp. indet.)	—	7	13	—	20
Araneida (Spiders) (spp. indet.)	49 (12)	38 (11)	56 (9)	6 (4)	149
Phalangida (Harvestmen) (spp. indet.)	23 (4)	8 (3)	17 (2)	—	48
CRUSTACEA, ISOPODA (Woodlice)					
Philoscia sp.	—	1	—	—	1
Armadillidium vulgare Latr.	—	—	1	—	1
MYRIAPODA, CHILOPODA (Centipedes)					
?Notophilidae (sp. indet.)	—	—	—	2	2
MOLLUSCA					
GASTROPODA (Snails) (spp. indet.)	—	1	2 (2)	—	3

Table 3. *Individual crop analyses. 0–7 days*

Crop No.	Date	*Sminthurus viridis*	*Forficula auricularia*	*Acrocephalus* spp.	Other Homoptera	Aphididae	Heteroptera	*Sitona puncticollis*	Other Curculionidae	Other Coleoptera	*Phytonomus* larvae	Lepidoptera larvae	*Acanthomyops niger*	Other Hymenoptera	Diptera	Other adult insects	Other larval insects	Araneida	Phalangida	Total animals	Seeds	Green leaves
1	16 June 1934	47	.	.	2	35	1	.	.	.	.	5	.	2	.	1	.	.	1	94	.	.
2	16 June 1934	31	.	.	.	57	.	.	.	.	.	6	.	1	.	.	.	.	.	95	.	.
3	26 June 1934	8	.	.	3	.	8	.	5	.	.	.	.	2	1	.	1	3	.	31	.	.
4	24 June 1935	.	.	3	9	2	.	.	14	.	73	4	.	1	2	4	.	.	.	112	.	.
5	24 June 1935	5	.	2	8	.	.	.	15	.	98	3	.	.	2	3	.	1	.	137	.	.
6	24 June 1935	.	.	.	2	.	.	.	.	.	57	3	.	1	3	1	1	.	.	68	.	.
7	4 July 1934	129	.	.	8	.	8	.	2	.	.	14	.	6	3	7	.	16	.	193	.	.
8	28 June 1935	18	9	2	.	13	.	.	2	1	24	5	.	.	1	.	.	2	.	77	+	+
9	28 June 1935	4	10	.	.	2	.	2	.	.	.	.	.	1	.	2	1	.	.	22	+	.
10	28 June 1935	116	6	2	2	6	.	.	.	4	1	2	.	2	.	.	4	7	.	152	.	.
11	28 June 1935	13	2	1	.	1	.	.	.	.	.	.	.	1	.	.	.	5	.	23	.	.
12	28 June 1935	40	.	.	.	3	.	1	.	.	.	8	.	.	.	.	3	2	.	57	.	.
13	22 June 1936	1	.	.	1	28	.	.	.	.	29	.	1	.	.	.	.	.	.	60	.	.
14	22 June 1936	.	.	.	.	41	.	.	.	.	18	.	.	.	.	.	.	.	.	59	.	.
15	25 June 1936	8	1	8	.	22	1	.	5	1	36	.	4	2	1	2	.	3	.	94	.	.
16	25 June 1936	2	1	.	3	17	.	.	.	.	98	1	.	.	.	.	.	3	.	125	.	.
17	25 June 1936	7	.	5	.	18	1	.	1	.	20	1	1	.	1	.	1	1	.	57	+	.
18	25 June 1936	15	.	.	19	24	.	.	1	1	21	1	3	.	1	.	.	1	.	87	.	.
19	26 June 1936	15	.	.	1	65	.	1	3	1	5	1	.	.	1	.	.	.	6	99	.	.
20	26 June 1936	21	.	.	1	45	.	6	1	.	9	5	.	1	.	2	1	.	8	100	+	.
21	26 June 1936	76	.	7	.	89	.	.	3	.	12	1	.	.	.	.	.	5	8	201	+	.
	Totals	556	29	30	59	468	19	10	52	8	501	60	9	20	16	22	12	49	23	1943		

Table 4. *Individual crop analyses.* 8–14 *days*

Crop No.	Date	*Sminthurus viridis*	*Forficula auricularia*	Acrididae nymphs	*Acocephalus* spp.	Other Homoptera	Aphididae and Aleyrodidae	Heteroptera	*Sitona puncticollis*	*Phyllobius viridiaeris*	Other Curculionidae	Other Coleoptera	*Phytonomus* larvae	Lepidoptera larvae	Formicoidea	Formicoidea cocoons + larvae	Other adult Hymenoptera	Diptera	Other adult insects	Other larval insects	Araneida	Phalangida	Other animals	Total animals	Seeds	Green leaves
22	22 June 1934	1	.	8	.	2	.	.	.	.	.	1	.	7	23	144	.	.	.	2	3	.	.	191	+	.
23	22 June 1934	2	.	8	.	.	1	6	.	.	1	.	1	3	34	96	.	2	.	.	1	.	.	155	.	.
24	2 July 1935	113	2	.	2	.	1	.	.	.	4	3	.	.	.	.	.	2	1	.	3	.	7	138	+	+
25	20 June 1934	3	.	.	.	5	5	5	.	2	1	1	.	4	18	41	.	1	.	.	.	.	.	86	.	.
26	20 June 1934	3	.	.	2	9	3	1	.	.	.	.	.	1	1	.	.	.	.	1	3	.	.	24	+	.
27	2 July 1936	62	.	.	.	1	3	.	7	.	2	2	13	1	.	.	1	.	.	2	.	.	.	94	+	.
28	2 July 1936	128	.	.	.	3	3	.	16	.	4	13	21	1	.	.	.	.	6	2	6	.	.	203	+	+
29	2 July 1936	107	.	.	.	3	.	.	14	.	4	8	35	1	.	.	.	1	.	5	5	.	.	183	+	.
30	26 June 1936	1	.	.	.	3	9	.	.	.	.	.	16	.	.	.	1	1	1	1	2	1	.	36	.	.
31	27 June 1936	1	.	.	.	1	13	.	.	.	1	.	12	.	.	.	.	.	.	.	.	.	.	28	.	.
32	10 July 1934	.	.	.	8	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	16	+	+
33	10 July 1934	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	2	+	.
34	10 July 1934	3	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	7	.	.
35	27 June 1934	62	.	2	3	30	.	100	.	135	.	3	66	.	17	.	12	13	10	3	6	.	.	462	+	+
36	9 July 1935	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	23	.	.
37	9 July 1935	.	.	.	6	1	.	.	10	.	.	2	.	3	.	.	3	2	2	5	.	.	.	34	.	.
38	9 July 1935	28	.	.	1	.	4	.	5	.	.	4	.	1	.	.	.	.	.	.	3	.	.	46	+	.
39	22 June 1934	78	.	.	.	7	216	20	.	.	4	.	44	1	4	.	7	3	.	3	2	.	1	390	.	.
40	5 July 1935	.	2	.	4	.	.	.	.	.	3	2	14	.	1	.	.	.	.	.	.	.	1	27	.	.
	Totals	611	4	18	26	69	259	132	52	137	25	39	222	24	98	281	24	25	20	24	38	8	9	2145		

Table 5. *Individual crop analyses.* 15–21 *days*

Crop No.	Date	*Sminthurus viridis*	*Forficula auricularia*	Acrididae nymphs	*Acocephalus* spp.	Other Homoptera	Aphididae and Aleyrodidae	Heteroptera	*Sitona puncticollis*	Other Curculionidae	Other Coleoptera	*Phytonomus* larvae	Lepidoptera imagines	Lepidoptera larvae	Formicoidea	Formicoidea cocoons	Other adult Hymenoptera	Diptera	Other larval insects	Araneida	Phalangida	Other animals	Indet. animal fragments	Total animals	Seeds	Green leaves	Flowers
41	8 July 1935	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	4	+	.	.
42	1 July 1936	.	.	1	1	6	.	4	.	2	4	1	10	7	.	.	3	.	.	11	.	.	+	50	+	+	.
43	4 July 1934	.	1	.	38	7	.	1	.	.	2	.	.	.	.	.	.	.	.	2	.	.	+	51	+	.	.
44	4 July 1934	.	1	.	18	2	.	.	.	4	1	.	.	5	.	.	1	.	2	.	.	.	+	34	+	+	.
45	21 July 1936	.	.	.	.	21	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	.	24	+	.	.
46	20 July 1935	10	.	.	.	.	.	.	.	2	1	.	4	.	6	1	.	.	.	9	.	.	+	33	+	+	+
47	20 July 1934	13	.	.	.	20	45	37	.	1	.	.	5	.	194	29	3	4	.	9	.	.	.	360	+	.	+
48	3 July 1936	1	.	.	.	.	.	.	2	.	5	.	.	1	.	.	.	.	.	3	.	.	+	12	+	.	.
49	3 July 1936	.	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	3	.	.	.
50	25 June 1934	.	.	.	.	.	10	.	.	2	1	27	.	.	.	.	2	.	.	1	.	1	.	44	+	.	.
51	25 June 1934	.	.	.	1	.	10	.	7	14	2	84	.	.	.	.	2	.	1	4	2	1	.	128	+	+	.
52	11 July 1935	38	1	.	.	1	.	.	.	.	1	2	.	.	324	1593	.	1	.	.	.	.	.	1961	+	+	.
53	17 Oct. 1934	.	.	.	1	2	3	12	.	1	1	.	.	1	.	.	1	1	.	15	15	13	.	66	.	.	.
54	5 July 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.
55	6 July 1934	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.
	Totals	64	3	1	59	60	68	54	9	26	19	114	19	17	524	1625	12	6	3	56	17	16		2772			

Table 6. *Individual crop analyses. Over* 21 *days*

e	Orthoptera	*Forficula auricularia*	Hemiptera	Curculionidae	Other Coleoptera	Lepidoptera larvae	Formicoidea	Other adult Hymenoptera	Diptera	Other adult insects	Other larval insects	Araneida	Chilopoda	Indet. animal fragments	Total animals	Seeds	Green leaves	Flowers	Roots
y 1934	.	.	5	.	.	.	2	1	3	1	1	.	.	.	13	+	+	.	.
y 1934	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	+	+	.	.
g. 1934	2	2	.	.	.	.	.	.	.	1	1	1	.	.	7	+	.	+	.
g. 1934	.	.	2	.	2	1	2	1	3	2	1	3	2	.	19	+	+	.	+
g. 1934	.	.	.	.	.	.	.	.	1	1	.	1	.	.	3	+	.	.	.
g. 1934	.	.	.	.	.	1	.	.	.	.	1	.	.	.	2	+	+	.	.
y 1935	1	.	2	.	18	.	1	.	.	.	1	1	.	.	24	+	.	.	.
g. 1937	.	.	.	7	1	.	7	.	.	.	.	.	.	+	15	+	.	.	.
1937	.	.	.	2	1	.	.	.	.	.	.	.	.	.	3	+	+	.	.
t. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
t. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
t. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.
t. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
t. 1935	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Totals	3	2	10	9	22	2	12	2	7	5	5	6	2		87				

Aston Tirrold, 24. SHROPSHIRE. Cressage, 27, 28, 29. HERTFORDSHIRE. Knebworth, 3, 4, 5, 6, 35, 47, 59, 60, 61. NORFOLK. Sandringham, 8, 9, 10, 11, 12; Crown Point, 30, 31; Wroxham, 62; Thornham, 63, 64; Raveningham, 65, 66, 67, 68, 69; Castle Acre, 13, 14; Witchingham, 15, 16, 17, 18, 40, 54. CAMBRIDGESHIRE. Six Mile Bottom, 56, 57. LINCOLNSHIRE. Denton, 43, 44. YORKSHIRE. Skelton, 37, 38. NORTHUMBERLAND. Longhirst, 7, 36. PERTHSHIRE. Elcho Park, 45. FORFARSHIRE. Edzell, 48, 49.

The differences between the individual crop contents shown in these tables are attributable to three factors. Two of them, namely the differences in food available to chicks in various localities and the time of death in relation to the last emptying of the crop, do not require comment. A third factor is found in the opportunity a chick may have for making a large meal. This factor applies particularly to crops in which one item predominates. When a particular source of food is concentrated and does not need searching for, it is probable that the crop is filled to greater capacity than at any time when feeding is at random. This occurs in crop No. 35 which contained 135 adult weevils of the species *Phyllobius viridiaeris* and also in those crops of the second and third age classes containing large numbers of ants and their cocoons. Before, however, considering partridge chick feeding habits in general, it is necessary to consider other aspects of the food analysis.

The volumes of the various animal groups in each age class are given in Table 7 from which it is evident that the abundance of the different kinds of food given in Tables 3–6 is by no means a good index of their importance as diet. Nor, however, is the volume a reliable index, since a few large animals, only eaten rarely, may come to occupy a disproportionally large place in the

volume figures. In assessing the importance of different food items it is necessary to consider as well a third measure: the frequency of occurrence.

Table 7. *Volumes of insects, etc. (c.c.) eaten by partridge chicks*

	1st week	2nd week	3rd week	Over 3 weeks
Sminthurus viridis	0·25	0·30	0·03	—
Acridiidae	—	0·45	0·02	—
Forficula auricularia	0·45	0·10	0·10	—
Homoptera (ex Aphids)	0·32	0·37	0·45	—
Aphididae and Aleyrodidae	0·63	0·35	0·10	—
Heteroptera	0·05	0·25	0·10	—
Sitona puncticollis	0·40	0·45	0·10	0·10
Phyllobius viridiaeris		0·80		
Other Curculionidae		0·15		
Other Coleoptera	0·03	0·30	0·30	0·05
Phytonomus larvae	2·95	1·05	0·50	—
Lepidoptera: Imagines	—	—	0·30	—
Larvae	1·45	0·70	1·20	—
Formicoidea: Imagines	0·01	0·15	0·60	—
Cocoons	—	1·20	1·75	—
Other Hymenoptera, Imagines	0·05	0·10	0·04	—
Diptera	0·05	0·05	0·01	—
Other insects: Imagines	0·06	0·15	—	—
Larvae	0·01	0·25	0·01	—
Araneida	0·05	0·10	0·20	—
Phalangida	0·15	0·05	0·40	—
Other animals	—	0·05	0·15	0·20
Indet. animal fragments	—	—	0·15	0·10
Totals	6·91	7·37	6·51	0·45

Table 8. *Plant seeds, etc., eaten by partridge chicks in each age class, with their abundance, frequency and volume* (c.c.)

	Volume (c.c.)					Numbers			
Seeds	1st week	2nd week	3rd week	Over 3 weeks	Total volumes	1st week	2nd week	3rd week	Over 3 weeks
Ranunculus sp.	—	0·25	0·05	—	0·30	—	108	21 (3)	—
Silene inflata	—	—	+	0·50	0·50	—	—	2	274
Cerastium vulgatum	—	0·03	—	—	0·03	—	3	—	—
Stellaria media	—	+	0·08	0·57	0·65	—	2 (2)	22 (4	173
Carophyllaceae (sp. indet.)	—	—	—	0·06	0·06	—	—	—	90 (2)
Myosotis arvensis	0·01	0·17	+	—	0·18	6	75	1	—
Calamintha acinos	0·05	—	—	—	0·05	1 fruit head	—	—	—
Polygonum sp.	—	0·01	+	0·04	0·05	—	1	1	5
Euphorbia exiqua	—	—	—	0·01	0·01	—	—	3	7
Carex sp.	—	—	—	0·85	0·85	—	—	—	3400
Alopecurus agrestis	0·01	—	0·04	0·02	0·07	2	—	14 (2)	5 (2)
Avena sativa	—	—	—	0·03	0·03	—	—	—	1
Holcus lanatus	—	—	0·01	—	0·01	—	—	7	—
Hordeum sativum	—	—	—	4·14	4·14		—	—	108 (4)
Lolium perenne	—	0·02	—	0·21	0·23	—	8	—	103
Lolium italicum		0·09	0·19	—	0·28	—	64	132 (6)	—
Festuca pratensis	—	—	1·38	0·07	1·45	—	—	613	32
Dactylis glomerata	—	—	—	0·20	0·20	—	—	—	171
Poa pratensis	0·22	0·10	2·12	0·35	2·79	613 (4)	148 (4)	2425 (3)	648 (4)
Poa trivialis	—	—	0·30	—	0·30	—	—	983 (2)	—
Triticum sp.	—	—	—	4·15	4·15	—	—	—	112 (4)
Dari	—	—	0·03	—	0·03	—	—	1	—
Maize	—	—	0·20	—	0·20	—	—	12 bits	—
Sp. indet.	—	—	0·60	—	0·60	—	—	185	—
TOTAL VOLUME OF SEEDS	0·29	0·67	5·00	11·20	17·16	622	409	4422	5129
Green leaves and grass	0·05	0·09	0·28	0·95	1·37	(1)	(4)	(5)	(8)
Flowers and buds	—	—	0·63	0·33	0·96	—	—	(2)	(2)
Roots	—	—	—	0·90	0·90	—	—	—	(3)
TOTAL VOLUME OF VEGETABLE MATTER	0·34	0·76	5·91	13·38	20·39				

(*b*) *Plant food.* Similar considerations apply to the plant food. The occurrence of plant food in the crops has been indicated in the previous Tables 3–6. The more detailed analysis of species eaten, mainly as seeds, with their abundance and volumes in each age class, is shown in Table 8.

Of all the seeds eaten only one species was common to all four groups: *Poa pratensis*, a common meadow grass. Although this seed is very small and consequently occupies a comparatively small volume, it must be considered an important item in the food. Wheat and barley (unripe) form a large part of the total volume eaten by those chicks over 3 weeks old. As already explained this is very likely due to the fact that corn only became available when this age was attained, since we examined no very young birds from corn fields. All the individual seeds eaten during the first periods are very small.

The most important feature emerging from a comparison of the animal and plant food of the chicks is the change from an almost completely animal diet in the first 2 weeks to a diet mainly vegetable, i.e. closely resembling that of adults (**1**) after the age of 3 weeks, the change taking place rapidly in the third week. The percentage volumes of plant and animal food are given in Table 9, which is reproduced graphically in Fig. 1. An inspection of the data given will show that similar figures would result using either abundance or frequency.

The comparatively sudden change from an animal to a vegetable diet is a striking proof of the fact stated in the previous paper (**1**) that insects are not an important food of the adult. This transition takes place in the summer months at the time when insects are most numerous and when it was found that adult crops contain the highest percentage of animal food. In the light of these facts it is difficult to give much credence to Collinge's hypothesis that the partridge has changed its food habits since he made his examination of crop contents (**2**). Instead, it might be said that the partridge changes its food habits during the third week of life, for, although insects are still abundant, it suddenly takes to vegetable food.

Table 9. *Percentage volumes of plant and animal food in partridge chick crops*

	0–7 days	8–14 days	15–21 days	Over 21 days
Plant food	4·7	9·3	47·5	96·7
Animal food	95·3	90·7	52·5	3·3

The predominantly animal diet of the first 2 weeks after hatching seems to be correlated with the habit of newly hatched chicks of pecking at moving objects. Thus hand-reared chicks show a distinct preference for any moving particles of food rather than stationary ones. With the change over to plant food this habit is largely lost and, except in summer, insects cease to form an important part of the partridge diet (**1**).

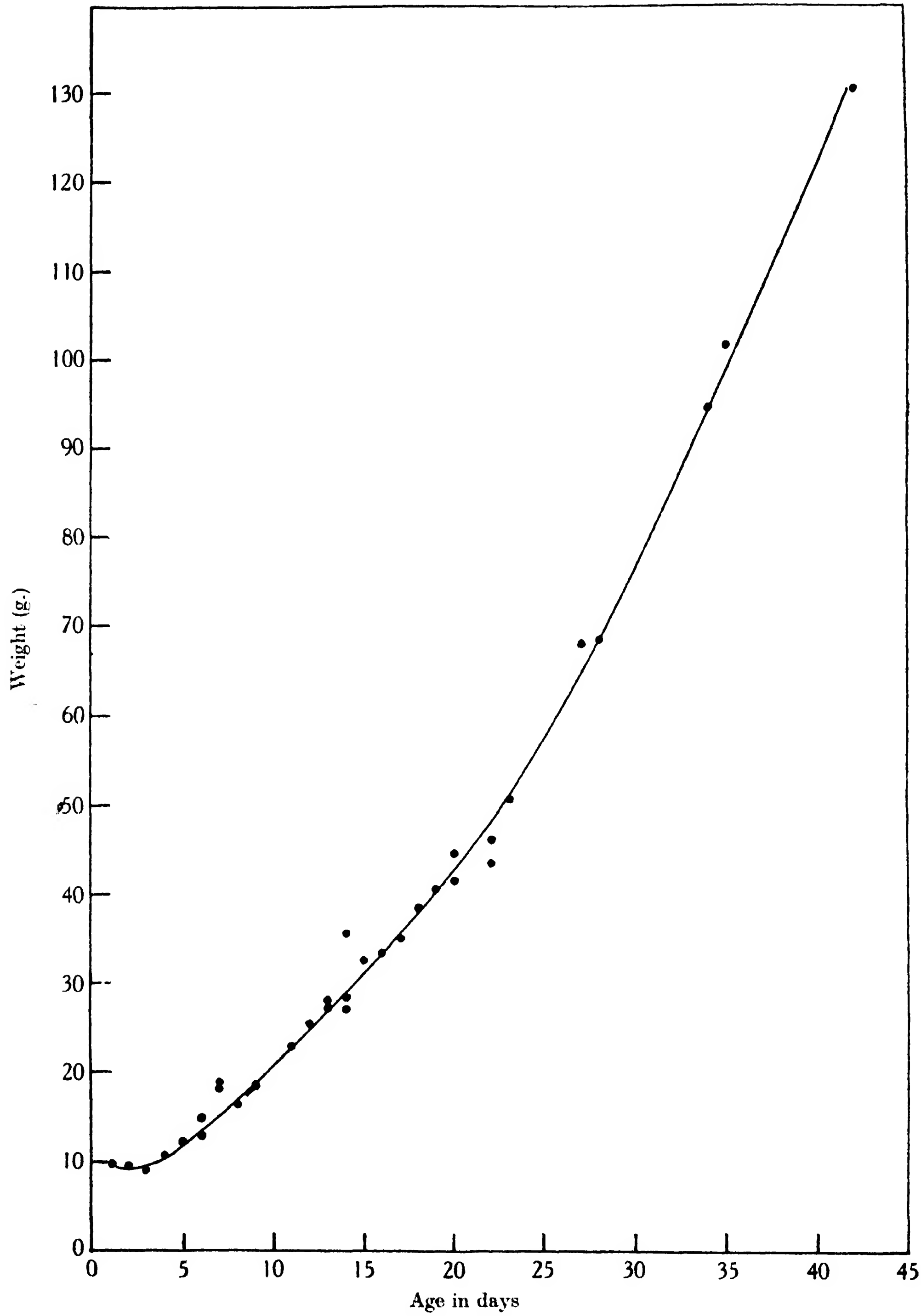

Fig. 2. Weights of partridge chicks at different ages. (The curve was drawn by eye.)

4. Evaluation of food items

It has been mentioned that to arrive at an estimate of the relative values, as food, of the various constituents of the crops, it is necessary to consider their abundance, volume and frequency of occurrence. This is the more necessary in the present case owing to the small number of crops available. Table 10 presents abundance and volume expressed, for comparison, as percentages, together with the frequency of occurrence of each group of animal species.

Table 10. *Percentage abundance and volume of insects, etc., in each age class, together with frequencies of occurrence*

Species or group of species	1st week			2nd week			3rd week		
	Abundance	Vol.	Frequency (21)	Abundance	Vol.	Frequency (19)	Abundance	Vol.	Frequency (15)
Sminthurus viridis	28·6	3·6	18	28·5	4·1	15	2·3	0·5	5
Acridiidae	—	—	—	0·8	6·1	3	0·1	0·3	1
Forficula auricularia	1·5	6·5	6	0·2	1·4	2	0·1	1·5	3
Homoptera	4·6	4·6	17	4·4	5·0	16	4·3	6·9	9
Aphididae	24·1	9·1	17	12·1	4·7	11	2·5	1·5	4
Heteroptera	1·0	0·7	5	6·2	3·4	5	1·9	1·5	4
Curculionidae	3·2	5·8	13	10·0	19·0	13	1·3	1·5	8
Other Coleoptera	0·05	0·4	5	1·8	4·1	10	0·7	4·6	10
Phytonomus larvae	25·8	42·7	14	10·3	14·3	9	4·1	7·7	4
Lepidoptera larvae	3·1	21·0	15	1·1	9·5	11	0·6	18·4	6
Formicoidea and cocoons	0·05	0·1	4	17·7	18·3	7	77·5	36·1	4
Other insects	4·1	2·5	17	4·3	7·5	12	1·4	5·5	8
Araneida	2·5	0·7	12	1·8	1·4	11	2·0	3·1	9
Phalangida	1·2	2·2	4	0·4	0·7	3	0·6	6·1	2
Other animals	—	—	—	0·4	0·7	3	0·6	4·6	9

From this table we may attempt to estimate the importance of the different groups of animals eaten. In the first week, only the larva of the weevil *Phytonomus* is eaten abundantly, frequently, and occupies a large volume in the crops. This species, according to Dr K. G. Blair, is probably *variabilis*, a common pest on clover and trefoils, on the leaves of which it feeds. These larvae are also an important item in the second week food. The larvae of Lepidoptera are also to be regarded as important contributors to the chick diet, for, though few are actually eaten, they occur in more than half of both first and second week crops and occupy a relatively large volume. On the other hand, the springtail, *Sminthurus viridis*, though eaten abundantly and often, occupies but little volume. Nevertheless, since it is evident that the chicks spend much of their time in catching this minute insect, it must also be regarded as an important item in the first and second week crops. Similar remarks apply to the Aphididae (with which are included in this table the Aleyrodidae). The Homoptera (excluding aphids) and the spiders, however, though eaten regularly and occurring in the majority of crops, are never abundant nor do they occupy much volume. Thus though regular items in the diet of partridge chicks they may be of relatively little importance.

As already pointed out, however, most of the important species found are those commonly present in the grass and clover habitats from which our specimens came. This applies particularly to *Phytonomus* and *Sminthurus*. Partridge chicks living in growing corn might show a different selection of insects, dependent on those most commonly available.

In the third week the most abundant insect food is composed of ants and their cocoons. These, however, are not eaten regularly. On hot days in July the ants and cocoons are very close to the surface of the nests, so that partridges have little difficulty in finding them. Once such a nest is opened the young partridge would be able to eat large numbers of ants and cocoons at one meal. The habit of eating ants and their cocoons is retained during adult life (**1**). Apart from this habit the eating of insects in general is probably a random process, the species most abundantly eaten being those most numerous or most easily available in the partridge habitat.

5. Summary

The contents of sixty-nine partridge chick crops were analysed, mostly from grass, clover and lucerne habitats. During the first 2 weeks after hatching the food is predominantly animal, during the third week a change occurs and from 3 weeks onward, food is almost entirely vegetable. Feeding on insects is probably random, the most important forms eaten being larvae of clover weevils, larvae of Lepidoptera, the springtail, *Sminthurus viridis*, Aphididae and ants. In evaluating the various constituents of the crops as to their importance as food, it was found necessary to consider not only the number of each species eaten, but also the volume and frequency of occurrence.

REFERENCES

1. **Middleton, A. D. & Chitty, H. (1937).** "The food of adult partridges, *Perdix perdix* and *Alectoris rufa*, in Great Britain." J. Anim. Ecol. 6: 322–36.
2. **Collinge, W. E. (1938).** "Food of the partridge." Nature, Lond., 141: 834.

ON THREE BIRD CENSUSES IN WOODLAND IN NORTHERN RHODESIA

By J. M. WINTERBOTTOM

(*With* 1 *Figure in the Text*)

THE censuses which form the subject of this paper were made by the method employed by the Americans whose figures are summarized by Forbes & Gross (**1**, and the papers cited in the bibliography therein) and by me in 1933, in a small count in scrub-woodland (**5**). On a front of 20 yd. every bird seen was counted. The routes followed native paths, but as the country was entirely uninhabited and only one party, of three people, was met, the results are unlikely to have been affected by human interference. The first count was made in the Chindeni hills between 8 and 9 a.m. on 23 October 1937. The day was overcast and rather cold. The distance covered was 4·6 miles (a cyclometer on a bicycle was used to measure distances), which gives an area of 33·5 acres. The second count was made north of Sasare between 7 and 8.45 a.m. on 30 October, over 7 miles (area, 51 acres). The day was clear and hot. The third count was along the south-eastern flank of the Chindenis on 3 November, between 8 and 9 a.m. The distance covered was 3·5 miles, giving an area of 25·5 acres. The day was hot.

These counts were made at the end of the dry season—indeed, the coolness of the air on the first day was undoubtedly due to rain having fallen somewhere within a radius of 50 miles.

The country through which the routes passed is composed almost entirely of *Brachystegia* woodland, mostly fairly well grown, with a sparse undergrowth of grass over which fires had passed. In occasional more open places, the grass was longer and here and there were clumps of bamboo, and anthills, with thickets of *Bauhinia* and other shrubs. The country is hilly and the ground for the most part plentifully sprinkled with large stones and fragments of rock. There was no surface water. These hills on which the third count was done are much lower than the others, with a larger percentage of relatively open country. As will be seen from the accompanying map, the greater part of the area lies in the eastern portion of the Petauke district, in the basins of the Lusangazi and Lusandwa rivers, both of which flow into the Luangwa, the latter by way of the Lupande. The confluence of the Luangwa and the Lupande is, however, off the map. The altitude is between 2500 and 3000 ft.

The total number of species in each census shows that although an hour's counting gave a very similar number of species, this was only about two-thirds of the total number in the region. On a total area of 110 acres, 287 birds were seen in three and three quarter hours. They belonged to at least 51 species (some individuals were not identified). This gives an average of 2·6 birds per acre,

according well with previous African results, as given by R. E. and W. M. Moreau (2) and by me (4), (5). The barren and waterless country apparently

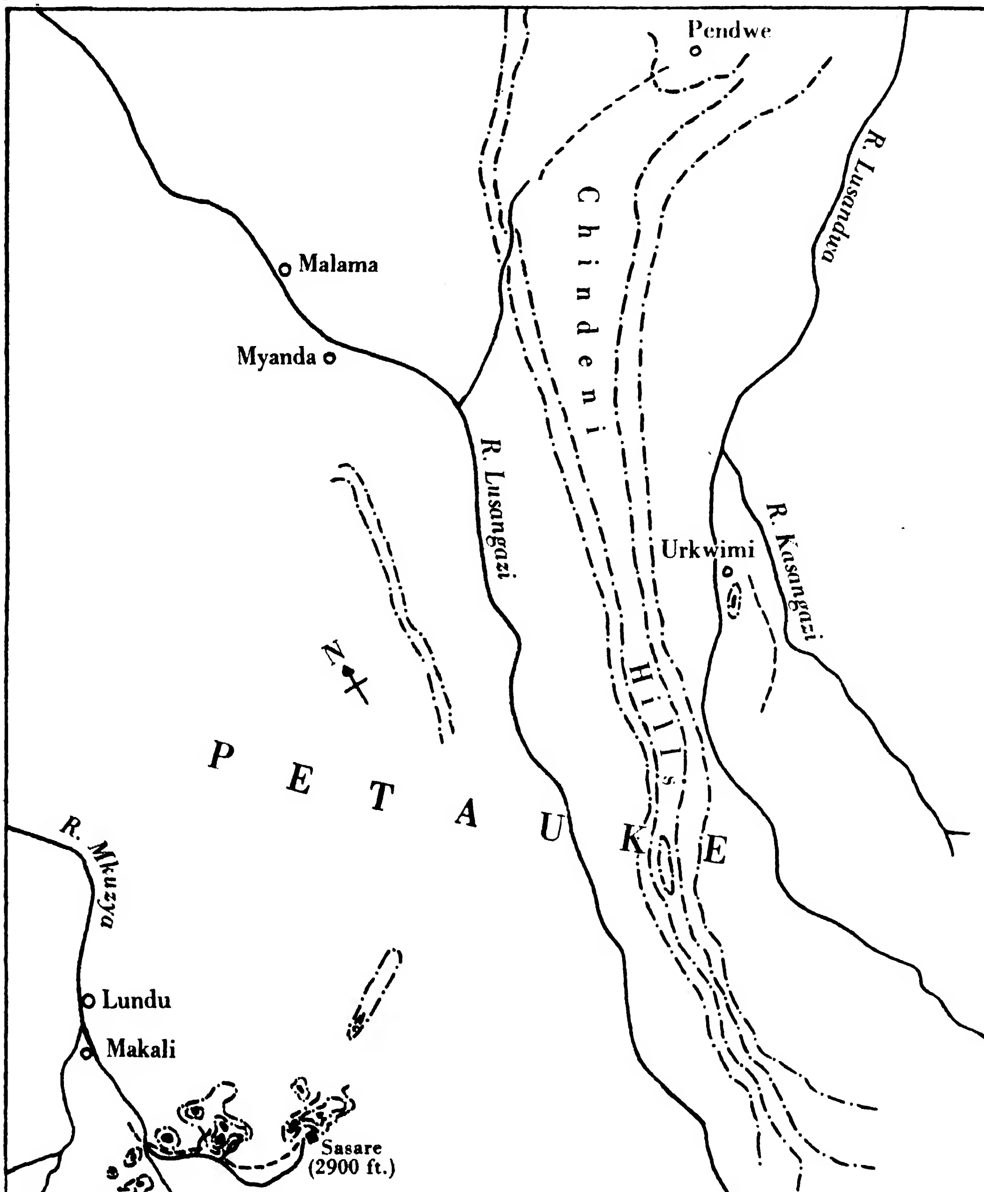

Fig. 1. Rough sketch-map of census region. (Scale ≑ 6·6 miles per inch.) Broken lines show census routes. Form-lines shown by dot and dash are very rough indications.

supports nearly as big a bird population as the mixed Tanganyika area investigated by the Moreaus. Only two species of Palaearctic migrants were included in the counts, the willow warbler (*Phylloscopus trochilus*), which was represented by eight individuals, thus standing ninth in order of abundance;

and the European bee-eater (*Merops apiaster*), of which a single example out of a party came within the area. The most numerous species was the Nyasa cordon-bleu (*Uraeginthus angolensis niassensis*), of which 31 examples were recorded, 24 of them in the third count, where the prevalence of thickets gave it the type of country best suited to it.

Second in order of abundance was the scarlet-chested sunbird (*Chalcomitra senegalensis gutturalis*), with 18 individuals. Next came the ubiquitous yellow-vented bulbul (*Pycnonotus tricolor* subsp.), with 15 examples.

Four other species are represented by ten or more individuals. Of the green-capped Eremomela (*E. scotops pulchra*) and the buff-breasted sunbird (*Cinnyris venustus falkensteini*), 13 examples of each were counted, while 10 each of the drongo (*Dicrurus a. adsimilis*) and the puff-back shrike (*Dryoscopus cubla hamatus*) were seen. All these species are common in woodland, the drongo being a wide-ranging species found almost everywhere. The first and the last two are amongst the commonest members of the bird parties that are such a characteristic feature of the woodland.

A list of all the species seen, with notes, arranged in the order followed by Sclater (**3**), is given on pp. 269-70.

The only really unexpected species in the whole census was the Palm-swift (*Cypsiurus parvus myochrous* (Rchw.)), but this is very common in places in the Luangwa valley where there are borassus palms (*Borassus aethiopium* Mart.) and wanders at times as far as Fort Jameson, where I recorded it six times between July 1932 and March 1935 (**6**).

It is important to realize that the figures obtained by this method of counting are only comparable if we assume that the relative speeds of the moving birds and the moving observer are constant. If the method is used to estimate actual bird density, we would have to assume that the rates of movement were roughly the same in birds and man. If birds were moving five times as fast as the observer, the density of birds would appear five times as great as if they moved at the same speeds. The bird parties, when not alarmed, move definitely more slowly than a walking man, probably not more than 2 miles an hour. The densities estimated are therefore lower for these species than in reality. For other species, such as doves and thrushes, there are as yet no data by which to check this point.

Summary

1. Three bird censuses made at the end of the dry season over strips of hilly woodland country covering 110 acres in the Eastern Province of Northern Rhodesia gave 287 birds of 51 species, an average of 2·6 per acre.

2. This agrees well with previous results for Africa.

3. The most abundant species was the cordon-bleu (*Uraeginthus angolensis niassensis* Rchw.), which was represented by 31 examples; six other species were represented by 10 or more individuals.

Species	Day 1	Day 2	Day 3	Total	Notes
Bateleur (*Terathopius ecaudatus* (Daud.))	.	.	5	5	Mainly an open country species
Lizard-buzzard (*Kaupifalco monogrammicus meridionalis* (Hartl.))	.	.	1	1	
East African shikra (*Accipiter badius polyzonoides* (Smith))	.	.	1	1	The commonest small hawk
Helmet-guineafowl (*Numida m. mitrata* Pall.)	.	.	6	6	A party
Cape turtle-dove (*Streptopelia capicola tropica* Rchw.)	2	.	1	3	Generally, the commonest dove
Blue-spotted wood-dove (*Turtur afer kilimensis* (Mearns))	.	1	.	1	A woodland species, unexpectedly scarce
Goaway-bird (*Corythaixoides c. concolor* (Smith))	.	.	1	1	An open country form
Brown parrot (*Poicephalus meyeri transvaalensis* Neum.)	2	2	.	4	The common parrot
Racquet-tailed roller (*Coracias s. spatulatus* Trim.)	3	.	.	3	
Broad-billed roller (*Eurystomus afer pulcherrimus* Neum.)	.	3	.	3	
European bee-eater (*Merops apiaster* L.)	1	.	.	1	
Grey-headed kingfisher (*Halcyon leucocephala swainsoni* Smith)	.	1	.	1	
Crowned hornbill (*Lophoceros melanoleucos suahelicus* Neum.)	.	1	.	1	A low level form, in the main; note no *L. nasutus*
East African wood-hoopoe (*Phoeniculus purpureus marwitzi* (Rchw.))	.	1	.	1	
Palm-swift (*Cypsiurus parvus myochrous* (Rchw.))	6	.	.	6	A foraging party from low levels
Black-collared barbet (*Lybius torquatus* subsp.)	.	.	1	1	
Yellow-fronted tinker-bird (*Pogoniulus chrysoconus extoni* (Layard))	1	1	2	4	
Greater honey-guide (*Indicator i. indicator* (Sparrm.))	2	.	.	2	
Cardinal woodpecker (*Dendropicus f. fuscescens* (Vieill.))	.	.	1	1	The common woodpecker
Arrow-marked babbler (*Turdoides jardinei kirki* (Sharpe))	4	.	2	6	
Yellow-vented bulbul (*Pycnonotus tricolor* subsp.)	5	6	4	15	
Pallid flycatcher (*Bradornis pallidus murinus* Finsch & Hartl.)	.	2	3	5	
Black flycatcher (*Melaenornis p. pammelaina* (Stanl.))	1	.	.	1	
Chin-spot flycatcher (*Batis m. molitor* Hahn & Küst.)	1	3	3	7	
Red Paradise flycatcher (*Tchitrea perspicillata plumbeiceps* (Rchw.))	.	3	.	3	Migrant; only present Sept. to March
Nyasa Kurrichane thrush (*Turdus libonyanus niassae* Rensch.)	2	2	1	5	
Willow warbler (*Phylloscopus trochilus* (L.))	4	2	2	8	
Green-capped Eremomela (*Eremomela scotops pulchra* (Boc.))	8	5	.	13	

Species	Day 1	Day 2	Day 3	Total	Notes
Tawny-cap grass-warbler (*Cisticola fulvicapilla ruficapilla* (Smith) ±*muelleri* Alex.)	1	.	.	1	
Tawny wren-warbler (*Prinia mistacea graueri* Hart.)	6	.	3	9	
White-breasted cuckoo-shrike (*Coracina pectoralis* (Jard. & Selby))	1	.	.	1	
Glossy-backed drongo (*Dicrurus a. adsimilis* Bech.)	4	1	5	10	
Southern helmet-shrike (*Prionops poliocephala* (Stanley))	7	.	.	7	One party
Puff-back shrike (*Dryoscopus cubla hamatus* Hartl.)	2	6	2	10	
Black-headed bush-shrike (*Tchagra senegala mozambica* (v. Som.))	.	2	1	3	
Sulphur-breasted bush-shrike (*Chlorophoneus sulfureopectus similis* (Smith))	1	.	.	1	
Black tit (*Parus niger* subsp.)	4	.	.	4	Race probably *insignis* Cab.
African golden oriole (*Oriolus auratus notatus* Ptrs.)	.	1	3	4	Chiefly a passage migrant, except in low level riverian cover
Black-headed oriole (*Oriolus monacha larvatus* Licht.)	.	5	.	5	The resident woodland oriole
Greater blue-eared glossy starling (*Lamprocolius chalybaeus sycobius* Hartl.)	1	.	4	5	
Scarlet-chested sunbird (*Chalcomitra senegalensis gutturalis* (L.))	9	5	4	18	
White-bellied sunbird (*Cinnyris talatala* Smith)	.	2	.	2	A low level species
Buff-breasted sunbird (*C. venustus falkensteini* Fischer & Rchw.)	5	8	.	13	Essentially a woodland species
Rock-sparrow (*Petronia superciliaris* (Blyth))	3	.	1	4	
Yellow-winged Anaplectes (*Anaplectes rubriceps* (Sund.))	5	2	.	7	A woodland species
White-winged whydah (*Coliuspasser a. albonotata* (Cass.))	.	4	3	7	A low level form
Bronze mannikin (*Spermestes cucullatus scutatus* Heugl.)	3	.	.	3	
Nyasa fire-finch (*Lagonosticta rubricata haematocephala* Neum.)	1	3	.	4	
Nyasa cordon-bleu (*Uraeginthus angolensis niassensis* Rchw.)	3	4	24	31	
Mozambique serin (*Serinus m. mozambicus* (Müll.))	7	.	.	7	
Yellow-breasted bunting (*Emberiza f. flaviventris* Stephens)	.	3	2	5	Essentially a woodland species
* Not identified (?)	7	7	3	17	
Total individuals	112	86	89	287	
Total species	31	27	26	51	

* This line has been inserted in proof without consultation with the author in view of a discrepancy found in the totals—Eds.

REFERENCES

1. **Forbes, S. A. & Gross, A. O. (1923).** "On the numbers and local distribution of Illinois land birds of the open country in winter, spring and fall." Bull. Ill. Nat. Hist. Surv. 14: 397–453.

2. **Moreau, R. E. & Moreau, W. M. (1931).** "The bird population of a settled valley in the West Usambaras, Tanganyika Territory." J. Ecol. 19: 64–74.

3. **Sclater, W. L. (1930).** "Systema avium Aethiopicarum." London.

4. **Winterbottom, J. M. (1933).** "Bird population studies. B. The population of twenty-one acres near Fort Jameson." Ostrich, 4: 67–70.

5. **Winterbottom, J. M. (1934).** "Bird population studies. 5. Five consecutive daily counts over 21 acres in Northern Rhodesia." Ostrich, 5: 60–2.

6. **Winterbottom, J.M. (1937).** "Bird population. 8. The avifauna of Fort Jameson, Northern Rhodesia, 1932–35." Proc. Zool. Soc. Lond. A, 107: 191–204.

THE FAUNISTIC RECOVERY OF A LEAD-POLLUTED RIVER IN NORTH CARDIGANSHIRE, WALES

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(*With* 1 *Figure in the Text*)

CONTENTS

1. Introduction

This study concerns the Rheidol, which is the largest river in north Cardiganshire, and along the course of which are some 43 mine workings (Map). The lead-mining industry here goes back to pre-Roman times; in the latter part of the nineteenth century it suffered severely from competition with larger undertakings, and shortly before the Great War all the mines had ceased working. During 1914–18 a few mines were reopened, but after the War these soon closed down once more. This paper is a study of the progressive recovery of the river fauna which followed.

The River Rheidol has its source on the western side of Plynlimon, the stream (Nant-y-llyn) from Llyn Llygad Rheidol being joined in the neighbourhood of Nant-y-moch by a number of mountain streams (Afon Hengwm, Afon Hyddgen, Afon Llechwedd Mawr and Afon Camdwr), and flows thence in a general southerly direction to Ponterwyd and Devil's Bridge, where it turns sharply westwards to reach the sea at Aberystwyth. The local rocks are grits, flags and shales of the Valentian and Bala series; metalliferous veins occur along the fault lines usually running east-north-east to west-south-west and are usually in the upper parts of the basins of the principal rivers.

Like all the rivers of the district, the Rheidol is rapid in flow, cutting deep gorges in the middle part of its course, and for the most part its bed is stony. Its lower valley is covered with boulder clay, and in quiet reaches its waters

are slightly turbid with the resulting mud; but for the most part the waters are clear and rapid and the banks are strewn with gritty pebbles brought down in time of flood. The general character of the river is such as to suggest that trout, salmon, etc., might occur in abundance. The neighbouring rivers, Dyfi, Leri and Teify, which are remarkably similar to the Rheidol in general physical character, have such fisheries and it is recorded in oral evidence taken in 1872 by the Commissioners on Rivers Pollution (1874*b*, p. 76) that early in the nineteenth century the Rheidol was a healthy river abounding in fish. However, when the study of the river was begun by Dr Carpenter in 1919, the lower reaches (below Rhiwfron) were absolutely devoid of fish life, the invertebrate fauna was extremely poor both in variety of species and number of individuals, and the vegetation was limited to slight coatings of moss and liverwort on some of the stones, and a certain amount of the Algae *Batrachospermum* and *Saccheria*.

The barren condition of the river has always been attributed to the extensive lead-mining, crushing and washing operations which have been carried on upon the banks of the river and some of its tributaries for hundreds of years past, though it is stated that serious pollution did not enter until the introduction of fine grinding machinery early last century. After this innovation, and despite the introduction of systems of settling ponds, a considerable amount of fine, lead-containing slimes found its way into the river. During periods of flood, when the water spread over the surrounding land, this material formed a film of mineral material over the vegetation, and numerous cases of poisoning of horses, cattle and poultry were attributed to this cause.

In the *Report* of the Rivers Pollution Commission appointed in 1868 are given a number of analyses of samples of water which had passed through settling ponds. The following example is taken therefrom (1874*a*, p. 42; and Frankland 1877, p. 834):

> Submitted to subsidence, 11·72% of the slime contained in the turbid water leaving the last settling pond at the "Powell United" lead mine near Aberystwyth, was deposited in the first 15 minutes, and 56·7% in the next six hours, leaving 31·58% still in suspension. 100 parts of the slime suspended in this water contained 1·38 part of lead as galena; but after subsidence for six hours and a quarter only 0·45 part of lead as galena remained in suspension. In connexion with this sample it is necessary to remark that the subsidence to which it had been submitted in the settling-ponds was more than usually effective, as is seen from the fact that 100,000 parts of the turbid water contained only 82·52 parts of suspended matter, whilst in the muddy waters from other mines more than 400 parts have been observed.

Whatever may be the physiological effect of these galena-containing slimes on domestic animals eating polluted vegetation, it has been proved by Carpenter (1924*a*, 1925) that the old theory, which attributed the killing of fish in polluted rivers to laceration of the gills and inflammation caused thereby by particles of galena grit, is without foundation. Her work has established beyond doubt that the poisoning of fish is due to the presence of the salts of certain heavy metals *in solution*. As a result of experiments in the field and in

the laboratory, it is concluded that these metals (in ionic state) react with some constituent of the mucus secreted by the gills with the formation of an impermeable pad over the latter, so that respiration is impeded and the fish dies of suffocation. As an example, it may be quoted that a concentration of 4 parts per 10 million of lead in water causes fatal results in minnows (*Phoxinus phoxinus*) in 36 hours. In still lower concentrations the time is longer and the fish may be able to get rid of the impeding film on the gills as rapidly as it is formed.

The solubility of lead sulphide (galena) is very low, and a saturated solution contains only 2·5 parts of lead per 10 million (the corresponding number for zinc sulphide—blende or black jack—is 4·0 parts per 10 million). It is obvious, therefore, that solutions of galena and blende can, as such, have no poisonous action on fish. It has been shown that galena when exposed to the combined action of air and water—which will obviously be much accelerated by vigorous agitation such as occurs in mine separation plants—is slowly oxidized to lead sulphate which has a solubility in water corresponding to 31·5 parts of lead per million. This explains why the effluents from active mine plants contain on the average 3 parts of lead per million in solution.

If slimes from an active mine are allowed to pass into a river the process of oxidation and solution of the resulting sulphate goes on continuously. The same process will occur on dumps of mine refuse which are such a prominent feature of the middle reaches of the Rheidol. During fair weather the oxidation will proceed and the oxidation products remain *in situ* until the first floods dissolve the sulphates and carry them into the river.

Fortunately, in course of time, the fine-grained material on the surface of many of the dumps becomes caked into a hard impenetrable mass from which water flows off before causing much action. Where the dump material is coarser and allows water to penetrate through, afterwards reappearing at the base of the dump as streamlets during prolonged wet weather, the amount of dissolved salts may be considerable. With the cessation of mining operations a river, therefore, tends to recover itself. By the action of floods the fine uncaked material may be washed from the dumps into the river and thence to the sea, while the heavier mineral particles tend to settle in the deeper and quieter parts where oxidation is prevented or delayed.

For the last nineteen years the Lower Rheidol has been kept under observation. The main changes which have taken place in the transition from an almost dead river to one supporting a relatively normal animal population are summarized below.

2. Surveys from 1919 to 1926

From 1919 to 1926 the work was done by Dr Kathleen Carpenter, who recorded her results in various papers (notably 1924*a*, 1925, and 1927*a*). During the period 1919–21 a thorough examination resulted in the finding of

only 14 species, distributed as indicated in Table 1. The list is almost entirely composed of insects and a few crustacean species. Vertebrata, Mollusca, Hirudinea, Oligochaeta and Platyhelmia are absent. During this period a number of estimations were made of the dissolved lead content of the river, the results varying from 2 to 5 parts per 10 million of water.

Table 1. *Species recorded from the Lower Rheidol previous to May* 1922 (*Carpenter*, 1924*a*, *p*. 14)

Crustacea (Copepoda, Ostracoda)	3	Plecoptera	2
		Ephemeroptera	1
Arachnida	1	Neuroptera	1
Hemiptera	2	Odonata	1
Coleoptera	2	Diptera	1
		Total no. of species	14

In the late spring of 1922 there was a long period of drought, and the level of the water fell considerably and many of the smaller tributaries dried up. The last two of the few mines that had been reopened during the War ceased working in 1920 and 1921 respectively. After the period of drought a number of further estimations were made of the diffusible lead content. From 24 October 1922 to 16 March 1923 it was nil in the majority of samples, and even in time of flood did not rise above 1 part in 10 million. (It should be noted, however, that later critical methods of estimating lead, at present in use, were not developed at this time.)

Following the improvement in the physical condition of the river came an almost immediate improvement in the fauna and flora. The previous Algal and Bryophyte vegetation was considerably augmented and at Penybont and elsewhere masses of *Callitriche verna* and *Ranunculus aquatilis* appeared. More striking still was the improvement in the fauna; the number of species was doubled and species previously recorded appeared in vastly greater numbers. Eight species of Trichopteran larvae appeared, and the flatworm *Polycelis nigra* was also taken, being the first planarian to be recorded from the Rheidol. The new conditions were traced 5½ miles upstream to Capel Bangor.

The species, increased to 29 in number, were distributed as in Table 2.

Table 2. *Species collected in the Lower Rheidol in and after May* 1922 *and up to March* 1923 (*Carpenter*, 1924*a*, *p*. 14)

Platyhelmia	1	Plecoptera	2
Crustacea (Copepoda, Ostracoda)	4	Ephemeroptera	2
		Neuroptera	1
Arachnida	1	Odonata	1
Hemiptera	2	Diptera	3
Coleoptera	4	Trichoptera	8
		Total no. of species	29

In the spring of 1924 two yearling trout were placed in a cage in the Rheidol, just above Capel Bangor, and survived from 4 February to 24 March, during which period the presence of lead was not determinable in the river.

Between 22 and 24 March heavy rain fell; on the 24th the lead content was 4 parts per 10 million and the fish died with the characteristic white film of mucus over the gills. (This increased amount of lead is explainable owing to the temporarily resumed workings at Erw-tomau.) This is the last record of so high a degree of pollution. From 1 June to 8 October in the same year six fish survived in the cage at the same place, no lead having been determinable in the water during this period. From this time onwards the Lower Rheidol is regarded by Carpenter as being chemically pure, though it must be borne in mind, as already indicated, that the critical methods of determining lead, which are at present in use, were not developed at this time.

Carpenter gives no later records of the fauna of the Rheidol as such, but (1927*a*) lists under the single heading "longer rivers of coastal area" the species from both the Lower Rheidol and Lower Ystwyth, the latter being a river with a very similar pollution history to that of the Rheidol. The combined list contains 57 species.

During the following year or two it appeared to us that further recovery might have taken place, and accordingly we carried out a further faunistic survey in some detail, from July 1931 to May 1932. Observations on the lead content were made concurrently by Prof. Campbell James. The survey resulted in the collection of 103 species, a remarkable increase; while the estimations of Prof. James indicated the intermittent continuance of a very low lead content.

3. Faunistic survey of the lower Rheidol, 1931–2

(*a*) *The regions examined*

A. *Penybont.*

The majority of the samples were taken just above Penybont bridge near Llanbadarn fawr, about a mile and a half from the mouth of the river at Aberystwyth. Above the bridge the river, which here is moderately shallow, runs a fairly rapid straight course for about a quarter of a mile. On the left side the water is of almost uniform depth, the bed is stony and there is little vegetation; but on the right side the bank, though not notched into large backwaters, is very irregular, and accordingly the river is broken up into numerous small regions, in some of which the depth is about 3 ft. close to the bank and the water comparatively slow moving, the bed being sand with large clumps of *Callitriche verna* and *Ranunculus aquatilis* growing in it. Around the fringe of these pools there is generally a fair amount of submerged grass (*Glyceria fluitans*). In the grass and waterweed of these areas numbers of mayfly nymphs, water beetles, and caddis larvae shelter. Many species, such as the naiad of the dragonfly *Cordulegaster annulatus*, live almost in the sandy bed. Here and there the water moves so slowly that there are deposits of dead leaves and other debris on the bottom, where numerous species shelter.

This stretch is easily the most richly populated area of the river, at any rate as far up as Capel Bangor. All the species listed were found in the Penybont

area except *Planaria vitta*, *Haemopis sanguisuga*, *Elmis aeneus* (all three species from Capel Bangor only), *Hydroporus erythrocephalus*, *Dytiscus punctulatus* (both from Parc-y-llyn only), and *Phryganea* sp. (Whitebridge only).

B. *The Whitebridge.*

At the white concrete bridge over the Rheidol, about half a mile above Llanbadarn, a portion of the river is separated from the main stream by a small island so that a kind of backwater is formed. This has a wide opening to the river near the bridge, and a narrow inlet higher up, through which the water enters to keep up a steady but slow flow through the backwater. This flow is always present even when the level of the river is below normal, and in flood

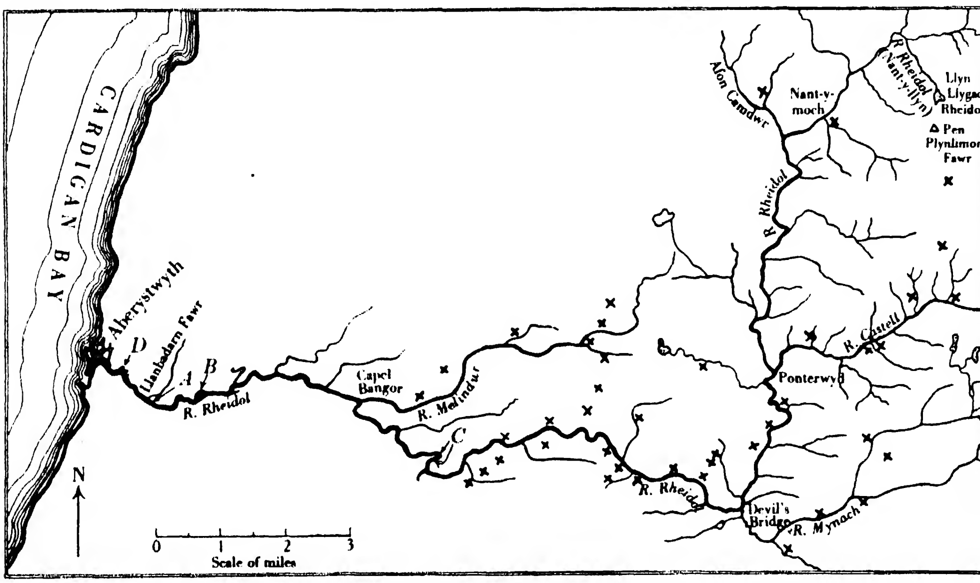

Fig. 1. Map of the River Rheidol and its tributaries. × Lead mines; ← sampling stations (*A*, *B*, *C*, *D*).

time the flow is almost as rapid as that of the main stream. The bottom of the backwater is chiefly covered with stones, dead leaves and other debris; near the bank are large beds of submerged grass, and here and there are clumps of *Callitriche verna* and *Ranunculus aquatilis*. However, it is the submerged grass (*Glyceria fluitans*) that shelters most of the fauna of this area. The species are essentially the same as those found at Penybont, but the number of individuals of some of the more quiet-water living species is greater. The single specimen of *Phryganea* sp. was taken here.

C. *Near Capel Bangor.*

Near Capel Bangor, about $5\frac{1}{2}$ miles from its mouth, the Rheidol makes an extremely acute bend. Near the apex of the angle and under the right bank, there is a deep pool where the water is almost stationary. Masses of *Callitriche*

verna grow upon the sandy bottom, which is carpeted with dead leaves from the overhanging trees, and other debris. Here the water net readily captures a great variety of species. A little higher up the river is shallow and rushes rapidly over large stones. Here web-spinning Trichoptera occur in great numbers, and almost every stone is plastered with *Simulium* larvae. This is the only part of the river where we have found *Planaria vitta*, *Elmis aeneus*, and *Haemopis sanguisuga* (a single specimen only of the last). *Rhyacophila* sp. occurred here in abundance, in contrast with its small numbers in the other three regions.

D. *Backwaters near Parc-y-llyn farm* (*Aberystwyth flats*).

About a quarter of a mile nearer the sea than Penybont bridge, and near Parc-y-llyn farm, the right bank of the river is indented by three small backwaters. These are generally in communication with the main stream, but there is very little circulation of water in them, and when the water-level is low they are separated off and become stagnant pools. In flood time, however, the river rushes through them, and so it is probable that any chemical changes that take place in the river at flood time exert their effect on the fauna of these regions just as much as upon that of the main stream.

Samples taken from these backwaters show that they are populated almost entirely by the same species that live in the main stream, the essential difference being that certain species, found rarely in the main stream, occur in the backwaters in large numbers—due apparently to the greater abundance of vegetation and the greater placidity of the water. Thus, *Limnaea pereger*, rarely found in the flowing waters of the main stream, occurs in numbers in the backwaters. Its presence here can hardly be due to any chemical distinction between the waters of the two regions, as it is also found in numbers in the Whitebridge Backwater, where it lives in water apparently identical chemically with that of the main stream.

These backwaters support masses of Algal and Bryophyte vegetation, in addition to *Callitriche verna*, and their bottoms are covered with mud and dead leaves in which live numbers of *Chironomus* larvae and Oligochaeta. Frogs spawn here, and in the spring countless tadpoles grow up and invade the main stream. Newts also occur, and insects usually associated with stagnant pools, such as *Hydrometra stagnorum* and *Nepa cinerea*. The beetles, *Hydroporus erythrocephalus* and *Dytiscus punctulatus*, were found only in this region.

(*b*) *Methods of investigation*

No precise quantitative sampling was attempted. Attention has been concentrated on collecting as many species as possible, whether common or rare, and noticing their general abundance, distribution and seasonal variation. The great majority of the species were taken in the water net, a few were taken

under stones, and a very small number by sieving out sand and mud from the bottom.

Each sample was taken in the following manner: First, specimens were captured of all surface dwellers such as *Gerris* and *Gyrinus*, and their general abundance noted. Then numbers of stones were taken up at various places, the animals on them captured; samples of the sand and mud on the bottom were brought home for sieving; and a canvas water net was thoroughly worked through the submerged grass and clumps of waterweed. The whole contents of the net were brought to the laboratory for thorough examination, all the species recorded, and notes were made of their relative abundance. All samples were taken in the same manner so that the results are reasonably comparative.

(c) *Number of samples*

July 1931. Four from A, one from C, two from D.

October 1931. One per week from A, one per week from B, one from C.

November 1931. One per week from A, one from B, three from D.

December 1931. As November until 22 December. No samples were taken between 22 December and 8 January.

January 1932. Two per week from A, one per week from B, one from C.

February 1932. As January.

March 1932. One per week from A, one from B.

April 1932. As March.

May 1932. One per week from A, two from B, one from D. Last sample taken 28 May.

(d) *Species recorded*

The species recorded in the 1931–2 survey are listed in Table 3, which also gives their relative and seasonal abundance. Our thanks are accorded to Prof. E. Balfour-Browne for help in naming the Coleoptera. The identification of the nymphs of Plecoptera, and Ephemeroptera, and Trichopteran larvae presents difficulties in the present state of knowledge; we thank Mr Martin E. Mosely for advice in dealing with the Trichopteran larvae, and Mr D. E. Kimmins, similarly, in regard to the nymphs of Ephemeroptera and Plecoptera, and for his identification of the species of Ephemeroptera which we have bred out. We have put after each named species the reference to a description with which our specimens are in agreement. These references are listed at the end of this paper. Specimens of nearly all the species have been preserved, and are being deposited in the British Museum (Natural History).

During the few years prior to the survey trout (*Salmo trutta*) had occasionally been seen in the river. In May 1932 they were observed as high up as Aberffrewd, about 7 miles from the river mouth, and lower down they were sufficiently abundant to lead to some fishing just above Penybont Bridge and at Aberystwyth flats. It was reported that a couple of sewin were taken in the latter region in August 1932.

Table 3. *Relative and seasonal abundance of species collected in the Lower Rheidol, July* 1931 *to May* 1932

A. Abundant. Large numbers in each sample.
B. Fairly numerous. Say 5–10 specimens in each sample.
C. Less common. Say 2–5 specimens in each sample.
D. Rare. Say 1 specimen in each sample.
E. Very rare. Only 1 specimen during the whole month.

Species	July	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
PLATYHELMIA									
Polycelis nigra Ehrenb. (**2**)	C	C	C	C	C	C	C	C	C
Planaria vitta Dugès (**1**)	.	.	.	.	D	D	.	.	.
OLIGOCHAETA sp.	C	C	C	C	C	C	C	C	C
HIRUDINEA									
Glossosiphonia complanata L. (**3**, p. 74)	.	.	.	D	D	.	D	.	.
Herpobdella atomaria Carena (**3**, p. 81)	.	.	.	.	D	D	.	E	.
Haemopis sanguisuga L. (**3**, p. 79)	.	.	.	.	E	.	.	.	.
MOLLUSCA									
Pisidium sp. (**5**, p. 7; **5a**, pl. 3)	.	.	.	.	C	C	C	C	D
Limnaea pereger Müller (**4**, p. 104)	.	.	.	.	.	C	.	C	B
Ancylastrum fluviatile Müller (**4**, p. 113)	.	.	.	.	.	E	.	C	.
Zonitoides nitidus Müller (**4**, p. 240)	.	.	.	.	.	E	.	.	.
CRUSTACEA									
Cyclops sp.	C	C	C	C	C	C	C	C	C
EPHEMEROPTERA									
Baetis sp. (**6**, p. 32)	.	.	A	A	A	A	B	.	.
Siphlonurus lacustris Etn. (bred out)	A	.	.	.	.	B	A	A	A
Ecdyonurus sp. (**6**, p. 31)	.	.	.	C	B	B	A	A	A
Leptophlebia sp. (**6**, p. 31)	.	.	.	.	.	.	.	C	D
ODONATA									
Cordulegaster annulatus Latr. (**7**, p. 31)	.	.	.	.	D	C	.	.	.
Pyrrhosoma nymphula Sulz. (**7**, p. 121)	.	.	.	C	B	C	C	C	D
Agrion puella L. (**7**, p. 116)	.	.	.	C	B	C	C	C	D
PLECOPTERA									
Perlodes sp. *a* (**8**, p. 83; **10**, p. 286)	.	.	C	B	B	C	.	.	.
Chloroperla sp. *a* (**8**, **10**)	.	.	E	E	C	B	C	C	D
Nephelopteryx nebulosa L. (**8**, p. 90; **10**, p. 305)	.	.	E	.	.	.	.	.	.
Isopteryx sp. *a* (**8**, p. 88; **10**, p. 300)	.	.	.	.	.	.	C	C	C
Leuctra sp. *a* (**8**, p. 92)	.	.	D	C	C	B	B	C	D
Protonemura sp. *a* (**8**, p. 93)	C	C	B	B	B	B	D	.	.
Amphinemura cinerea Morton (syn. *A. cinerea* Oliv. **8**, p. 95)	.	.	.	C	C	C	.	.	.
Nemurella inconspicua Pict. (syn. *N. pictetii* Klp. **8**, p. 95)	.	.	.	.	.	.	E	.	.
HEMIPTERA									
Hydrometra stagnorum L. (**9**, p. 148)	C	.	.	.	.	.	.	C	C
Gerris lacustris L. (**9**, p. 156)	C	.	.	.	.	.	.	C	C
G. najas De G. (**9**, p. 154)	D	.	.	.	.	.	.	.	C
Velia currens Fab. (**9**, p. 149)	A	B	.	.	.	.	.	.	C
Nepa cinerea L. (**9**, p. 327)	.	.	.	D	D	.	.	.	D
Notonecta glauca L. (**9**, p. 329)	B	B	B	.	.	.	B	B	C
Corixa geoffroyi Leach (**9**, p. 333)	B	B	.	.	.	.	.	.	C
Corixa sp. *a*	C	.	.	.	.	.	.	.	.
Corixa sp. *b*	.	.	B	B	B	B	C	.	.
Corixa sp. *c*	.	.	B	B	B	B	B	B	B
Corixa sp. *d*	.	.	.	.	C	.	.	.	.
Corixa sp. *e*	.	.	.	.	.	.	.	D	.
NEUROPTERA									
Sialis sp. (**10**, p. 321)	.	.	.	C	C	B	B	C	.
LEPIDOPTERA									
Sp. larva	.	.	.	.	.	E	.	.	.

Table 3 (*cont.*)

Species	July	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Ma
TRICHOPTERA									
Rhyacophila dorsalis Curt. (bred out)	D	D	D	D	C	C	D	D	.
Hydropsyche sp. *a*	.	.	D	C	C	C	C	D	D
Polycentropus flavomaculatus Pict. (**11**, p. 230)	C	C	C	B	B	B	C	D	.
Plectrocnemia conspersa Curt. (**11**, p. 230)	.	.	.	C	C	.	.	.	.
Beraeodes minuta L. (**11**, p. 243)	.	.	.	C	C	C	D	D	.
Phryganea sp. *a* (**11**, p. 238)	.	.	.	.	.	E	.	.	.
Sericostoma personatum Spence (bred out)	.	.	.	D	C	C	C	D	D
Limnophilus marmoratus Curt. (bred out)	.	.	.	C	B	B	C	C	D
Limnophilus sp. *a*	E	.	.	.	.	.	.	E	.
Limnophilus sp. *b*	.	.	.	E	.	.	.	.	.
Limnophilus sp. *c*	.	.	.	.	.	D	D	.	.
Limnophilus sp. *d*	.	.	.	.	.	.	.	D	.
Limnophilus sp. *e*	.	.	.	.	.	.	.	D	.
Anabolia nervosa Leach (**11**, p. 256) (bred out)	A	.	.	.	.	C	B	B	A
Halesus sp. *a*	.	.	.	C	B	A	A	B	.
Gen. *a*, sp. *a*	D	.	.	C	C	C	.	E	.
Glossosoma sp. *a* (pupa) (**11**, p. 290)	.	.	.	D	.	.	.	.	.
COLEOPTERA*									
Haliplus ruficollis De G. (**12**, p. 155; **14**, p. 16)	C	C	.	.	.	.	.	.	.
H. lineatocollis Marsh. (**12**, p. 156; **14**, p. 17)	C	C	.	.	.	.	D	.	.
H. wehnckei Gerh. (**14**, p. 18)	.	.	.	.	.	.	.	C	.
Haliplus sp. *a*	C	.	.	.	.	.	.	.	.
Laccophilus interruptus Panz. (**12**, p. 161)	.	.	.	.	.	.	E	.	.
Deronectes latus Steph. (**12**, p. 170)	.	.	.	.	.	D	.	D	D
D. elegans Panz. (**16**; **16a**, p. 177)	.	.	.	D	C	C	D	D	C
D. 12-pustulatus F. (**12**, p. 171)	C	.	.	D	.	.	C	C	C
Coelambus inaequalis F. (**12**, p. 168)	.	.	.	.	.	.	E	.	D
Hydroporus pictus F. (**12**, p. 176)	C	C	C	C	C	.	D	C	C
H. palustris L. (**12**, p. 182)	B	B	B	B	B	B	B	B	B
H. lepidus Ol. (**12**, p. 177)	.	.	.	C	C	B	B	C	C
H. vittula Er. (**12**, p. 181)	.	.	.	.	.	.	E	.	.
H. rivalis Gyll. (**12**, p. 177)	.	.	.	.	.	.	.	D	.
H. davisii Curt. (**12**, p. 178)	.	.	.	.	.	.	.	D	.
H. erythrocephalus L. (**12**, p. 182)	.	.	.	.	.	.	.	C	C
Hydroporus pubescens Gyll. (**12**, p. 185)	.	.	.	.	.	.	.	.	E
Hydroporus sp. *a*	D	.	.	.	.	.	.	.	.
Ilybius fuliginosus F. (**12**, p. 198)	C	C	.	.	.	.	.	C	C
I. ater De G. (**12**, p. 199)	.	.	.	.	.	.	.	.	E
Agabus bipustulatus L. (**12**, p. 196; **14**, p. 19)	.	.	.	D	.	D	D	.	.
A. didymus Ol. (**12**, p. 193)	.	.	.	D	C	C	C	D	C
A. sturmii Gyll. (**12**, p. 195)	C	C	.	.	D	C	D	.	D
Platambus maculatus L. (**12**, p. 197)	C	.	.	E	.	E	.	.	D
P. maculatus L. larva ? (**15**, p. 37)	.	.	.	.	.	.	.	.	.
Colymbetes fuscus L. (**12**, p. 203)	.	.	.	.	.	.	.	D	E
Dytiscus marginalis L. (**12**, p. 205)	D	.	.	.	.	.	.	D	D
D. marginalis larva (**12**, p. 204)	C	.	.	.	C	C	C	C	.
D. punctulatus F. (**12**, p. 204)	.	.	.	.	.	.	.	.	E
Helophorus viridicollis Steph. (**14**, p. 31)	.	.	.	E	.	.	.	.	.
Helophorus sp. *a* (**12**, p. 233; **14**, p. 29)	D	.	.	.	.	.	.	.	.
Laccobius alutaceus Thoms. (**14**, p. 27)	.	.	.	E	.	.	.	.	.
Gyrinus natator Scop. (**12**, p. 215)	B	C	.	.	.	.	.	C	B
Gyrinus sp. larva (**12**, p. 211)	.	.	.	D	D	C	.	.	.
Elmis aeneus Mull. (**13**, p. 376)	.	.	.	.	.	.	D	.	.
E. volkmari Panz. (**13**, p. 376)	.	.	.	C	C	C	D	D	.

* Examples of all the forms to which specific names are here assigned have been seen and confirmed Prof. F. Balfour-Browne, with the exception of *Dytiscus marginalis* (larva and imago), *Dytiscus punctulatu Gyrinus natator*, and the specimens of *Elmis*. The material was not all submitted to him, so that the write alone are responsible for the indication of seasonal occurrence. The (coleopteran) specimens are imagines, excej where otherwise stated.

Table 3 (*cont.*)

Species	July	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
DIPTERA									
Tipula sp. (**19**, p. 944; **18**, p. 68)	.	.	.	.	D	D	.	.	.
Tabanus sp. (**19**, p. 946; **18**, p. 149)	.	.	.	.	D	D	.	D	.
Simulium sp. (**19**, p. 946; **17**, p. 176; **18**, p. 107)	A	B	C	C	C	B	B	.	A
Chironomus sp. (**19**, p. 945; **17**, p. 139)	B	B	B	B	B	B	B	B	B
Tanypus sp. (**19**, p. 945; **17**, p. 152)	C	C	C	C	C	C	C	C	C
Ceratopogon sp. (**19**, p. 945; **17**, p. 155)	.	.	.	D	D	.	.	D	.
ARACHNIDA									
Hydracarina	.	.	.	.	.	.	.	C	B
VERTEBRATA									
Anguilla anguilla L. (as *Anguilla vulgaris* in **21**, p. 241; **22**, p. 49)	B	.	.	.	.	D	C	C	C
Gasterosteus aculeatus L. (**20**, p. 238; **22**, p. 61)	C	C	C	C	C	B	B	B	B
Triturus vulgaris vulgaris L. (syn. *Molge vulgaris*, **23**, p. 68; **24**, p. 38)	D	.	.	.	.	D	D	D	D
Rana temporaria temporaria L. (tadpoles) (**23**, p. 89)	B	.	.	.	.	.	.	B	B
R. temporaria temporaria L. (frogs) (**23**, p. 73; **24**, p. 39)	.	.	.	.	.	.	C	C	.

(*e*) *Relation of lead concentration to the fauna*

During the period of the survey Prof. Campbell James periodically examined samples of water from the Lower Rheidol, using critical methods. A large number of analyses were made of river water taken under various conditions at different points in the region surveyed. Under normal conditions dissolved lead to the amount of 2 parts per 100 million was present, rising to 1 part per 10 million during flood periods. The lead concentration was never found to exceed the latter figure. The following are representative analyses:

Date	Station	Condition of river	pH	Total solids (Parts per 100,000)	Lead (Parts per 10,000,000)
14 Aug. 1931	Penybont Bridge	Full flood	6·6	4·6	1·0
20 Aug. 1931	Aberystwyth Flats	Flood cont.	6·6	4·5	1·0
23 Oct. 1931	Lovesgrove	Medium	6·7	5·0	0·5
6 Jan. 1932	Aberystwyth Flats	Full flood	—	9·0	1·0
10 Feb. 1932	Aberystwyth Flats	Low water	—	—	0·2
21 June 1932	Aberystwyth Flats	Low water	6·7	3·6	0·2
28 Oct. 1932	Aberystwyth Flats	Medium after flood	6·7	3·4	0·3

The water at Aberystwyth flats during a flood period, 31 March 1932, contained 2·6 parts per 100,000 of filterable solid material in suspension. Analysis of this suspended matter indicated that it contained 2 parts per 10 million of lead, 19 parts per million of iron, the remainder being silica (estimated on the volume of filtered water). The filtered water contained 0·25 part of lead per 10 million. This result indicates that the suspended matter contains only very slight traces of lead.

The remarkable increase in the richness of the fauna would thus appear to be associated with the persistence of conditions with only a reduced amount of lead in solution. It was evident, however, from the analyses of Prof. James that the river was still liable to slight intermittent pollution as a result of heavy rains washing out lead sulphate from the lead dumps; but the lead content of the river never rose to the relatively high values reached up to 1924.

This was due mainly to the closing down of the mines. And although the mine dumps still remained a source of pollution, it appeared likely that time had lessened the danger of pollution from this source. While great reserves of galena doubtless still remain deep down in the dumps it is possible that the lead near the surface has been largely removed, and that consolidation of the surface and the growth of vegetation has tended to hinder access of the weathering agents to the reserves.

When a flood occurs it is generally of short duration, the river level returning to normal in 3 or 4 days, or at most, a week. One of the writers (J. R. E. Jones) has shown that under laboratory conditions a lead concentration of 1 part in 10 million is directly fatal to the stickleback, *Gasterosteus aculeatus*; but an exposure of 14 days is necessary, on an average, before death occurs. If the fish is removed from the solution a reasonable time before death, and placed in untreated water, complete recovery occurs. Thus it appeared that the existence of this fish in the river depended on the shortness of the pollution periods. It is quite possible that a period of very heavy rain extending over 2 or 3 weeks might maintain the lead content of the river at 1 part per 10 million for this long and destroy all the sticklebacks in the river. No such period of prolonged flood occurred during the period under review.

The summer of 1936 was unusually wet, and was followed by an autumn of heavy rainfall. During October, November and December of the same year the river, though not actually in flood, was for long periods much above its normal level. The chances of pollution from the mine dumps were thus at a maximum and it was thought desirable, therefore, to carry out a further survey following this period. This survey was done by Mr Harry Evans, a Zoology Honours student, under the supervision of the writers, during the period December 1936 to April 1937 inclusive. Samples were taken at approximately fortnightly intervals from two (A and B) of the four stations surveyed in 1931–2. Only 68 species were recorded as against 104 species in the 1931–2 survey; but these comprise all the commoner forms found in the earlier period, including the stickleback, and the difference in number is due to the absence of many of those forms which occurred but rarely in the earlier survey. This might be expected, since Mr Evans's samples were 11 in number and collected from two localities compared with 74 samples in 1931–2 from four localities.

The number of individuals present, as distinct from the number of species, was of the same order as at the time of the earlier survey and the absentee species cannot be considered as of significance in relation to pollution. We can say with confidence that the river retains the healthy condition evidenced in 1932, in spite of heavy rain and periods of high water-level. Chemical evidence is entirely in agreement: in July 1937 Prof. James reported that while one, at least, of the streamlets which flow from the mine dumps into the river continued to be polluted with lead, the dilution by the mainstream was so great that there was no detectable degree of pollution of the river in any part of its course.

One of the writers has shown (Appendix) that the stickleback is among the animal forms most sensitive to lead, so that the river is not only free now from danger from lead pollution to its fauna during normal periods, but even the heaviest floods which are likely to occur seem to be without appreciable effect.

Nevertheless, as compared with some rivers, the fauna is not rich, and for this an explanation other than that of metallic pollution must be sought. The stream is swift and there is a lack of silt in its bed; there is a remarkable scarcity of lime; and the *p*H is low. Crustacea, Mollusca, and Hirudinea are very poorly represented. In laboratory experiments, however, the leech, *Haemopis lateralis*, survived for 18 days in a 3 parts per million solution of lead. The scarcity of Crustacea and Mollusca may well be associated with the scarcity of lime. The *p*H of the water has been observed at Penybont and elsewhere from time to time, and varies between 6·6 and 6·8.

At the time of writing (October 1937) young sticklebacks are observable in considerable numbers at Penybont, as also are large numbers of *Ancylastrum fluviatile*, another of the forms most sensitive to lead. We may conclude that the fauna of the Lower Rheidol has very materially, perhaps fully, recovered from the effects of the metallic pollution from which it suffered in association with the lead-mining industry.

4. Summary

1. From 1919 to 1921, the Lower Rheidol River only yielded 14 species of animals, all of them Arthropoda, in a careful survey made by Carpenter. During this period estimations of dissolved lead in the water revealed the presence of 2–5 parts of lead per 10 million of water.

2. From 1922 to the present time it would appear that lead has been indeterminable, or in the order of 2 parts per 100 million, except during flood periods. In one such period in 1924 Carpenter recorded 4 parts per 10 million, but no estimation exceeded 1 part per 10 million during the 2 years following. From June 1931 to the present time no greater flood concentration than 1 part in 10 million has been observed by Prof. James.

3. With the reduction in the amount of dissolved lead has been associated a steady improvement in the fauna. During the year following May 1922 the number of species recorded by Carpenter increased to 29, while the survey of July 1931 to May 1932 yielded 103 species, a fauna which appears to have remained stable since.

4. The Appendix gives the survival times of a number of species in a 3/1,000,000 solution of lead (as lead nitrate). The figures have some value as suggesting indices of pollution.

5. The stickleback (*Gasterosteus aculeatus*), which is one of the most sensitive to lead of the animals found in the Rheidol, was found, in laboratory experiments, to be killed after 14 days exposure to 1 part lead per 10 million of water.

This is the maximum concentration which has been observed in the Lower Rheidol for some years, even during flood, and the normal content is of the order of only 2 parts per 100 million, a concentration that the fish seems able to withstand indefinitely. It would appear therefore, that, provided no abnormal flood periods occur, there should be little direct danger to fish (at any rate, stickleback) life. And from the 1936–7 survey, made after a summer of exceptionally heavy rainfall, it appears that even when the river continues well above its normal level over long periods, there is now no appreciable effect upon the fauna. This has recovered very materially, we think fully, from the effects of the metallic pollution. Since 1932, trout have been sufficiently abundant to lead to some fishing.

REFERENCES

A. *Literature about the fresh-water fauna of Cardiganshire in relation to lead-mining*

Carpenter, K. E. (1922). "The fauna of the Clarach stream (Cardiganshire) and its tributaries. A preliminary investigation of the problem of lead pollution." Aberystwyth Stud. 4: 251–8.

Carpenter, K. E. (1923). "Distribution of *Limnaea pereger* and *L. truncatula*." Nature, Lond., 112: 9.

Carpenter, K. E. (1924a). "A study of the fauna of rivers polluted by lead mining in the Aberystwyth District of Cardiganshire." Ann. Appl. Biol. 11: 1–23.

Carpenter, K. [E.] (1924b). "Notes on the history of Cardiganshire lead mines." Aberystwyth Stud. 5: 99–103.

Carpenter, K. E. (1925). "On the biological factors involved in the destruction of river-fisheries by pollution due to lead-mining." Ann. Appl. Biol. 12: 1–13.

Carpenter, K. E. (1926). "The lead mine as an active agent in river pollution." Ann. Appl. Biol. 13: 395–401.

Carpenter, K. E. (1927a). "Faunistic ecology of some Cardiganshire streams." J. Ecol. 15: 33–54.

Carpenter, K. E. (1927b). "The lethal action of soluble metallic salts on fishes." Brit. J. Exp. Biol. 4: 378–90.

Carpenter, K. E. (1930). "Further researches on the action of metallic salts on fishes." J. Exp. Zool. 56: 407–22.

Frankland, E. (1877). "Experimental researches in pure, applied, and physical chemistry." London.

James, T. C. (1937). Report of West Wales Rivers Pollution Sub-committee. Min. Agr. Fish. Standing Committee on River Pollution, Serial No. 779. London.

Rivers Pollution Commission appointed in 1868. Fifth Report (1874). (*a*) Vol. 1, Report and Maps. (*b*) Vol. 2, Evidence.

B. *Literature used for identification of species*

Platyhelmia.

(1) **Ullyott, P. (1932).** "Notes on *Planaria vitta* Dugès." Quart. J. Micr. Sci. 75:483–94.

(2) **Whitehead, H. (1922).** "The British fresh-water Planarians (Tricladida)." Essex Nat. 20: 1–20.

Hirudinea.

(3) **Johansson, L. (1909).** "Hirudinea", in Brauer's "Süsswasserfauna Deutschlands". Heft 13. Jena.

Gastropoda.

(4) **Ellis, A. E. (1926).** "British Snails. A guide to the non-marine Gastropoda of Great Britain and Ireland Pliocene to Recent." Oxford.

Lamellibranchiata.

(5) **Rimmer, R. (1907).** "The land and freshwater shells of the British Isles." Edinburgh.

(5a) **Stubbs, A. G. (1907).** "Illustrated index of British freshwater shells." Leeds

Ephemeroptera.

(6) **Klapálek, Fr.** (1909). "Ephemerida", in Brauer's "Süsswasserfauna Deutschlands". Heft 8. Jena.

(6a) **Mosely, M. E.** (1921). "The dry-fly fisherman's entomology." London.

(10) **Rousseau, E.** (1921) as below.

Odonata.

(7) **Lucas, W. J.** (1930). "The aquatic (naiad) stage of the British dragonflies (Paraneuroptera)." Ray Society, London.

Plecoptera.

(8) **Klapálek, Fr.** (1909). "Plecoptera", in Brauer's "Süsswasserfauna Deutschlands". Heft 8. Jena.

(6a) **Mosely, M. E.** (1921) as above.

(10) **Rousseau, E.** (1921) as below.

Hemiptera.

(9) **Saunders, E.** (1892). "The Hemiptera Heteroptera of the British Islands." London.

Neuroptera.

(10) **Rousseau, E.** (1921). "Les larves et nymphes aquatiques des insectes d'Europe." Vol. 1. Brussels.

Trichoptera.

(11) **Ulmer, G.** (1909). "Trichoptera", in Brauer's "Süsswasserfauna Deutschlands". Hefte 5 und 6. Jena.

(6a) **Mosely, M. E.** (1921) as above.

(10) **Rousseau, E.** (1921) as above.

Coleoptera.

(12) **Fowler, W. W.** (1887). "The Coleoptera of the British Islands." Vol. 1. London.

(13) **Fowler, W. W.** (1889). Ibid. Vol. 3.

(14) **Fowler, W. W. & Donisthorpe, H. St J.** (1913). Ibid. Vol. 6 (Suppl.).

(15) **Reitter, E.** (1909). "Coleoptera", in Brauer's "Süsswasserfauna Deutschlands". Hefte 3 und 4. Jena.

(16) **Balfour-Browne, F.** (1919). "On *Deronectes depressus*, Fab., and *elegans*, Panzer." Ann. Mag. Nat. Hist. 3: 293–308.

(16a) **Balfour-Browne, F.** (1930). "The aquatic Coleoptera of Caithness and Sutherland. With some remarks upon species and varieties." Scot. Nat. 1930: 171–88.

Diptera.

(17) **Miall, L. C.** (1903). "The natural history of aquatic insects." London.

(18) **Grünberg, K.** (1910). "Diptera", Erster Teil, in Brauer's "Süsswasserfauna Deutschlands". Heft 2*a*. Jena.

(19) **Ward, H. B. & Whipple, G. C.** (1918). "Fresh-water biology." New York.

Pisces.

(20) **Day, F.** (1880–4). "The fishes of Great Britain and Ireland." Vol. 1. London.
(21) Ibid. Vol. 2.

(22) **Norman, J. R.** (1935). "Fishes" in "List of British vertebrates". Brit. Mus. (Nat. Hist.). London.

Amphibia.

(23) **Tornier, G.** (1909). "Amphibia", in Brauer's "Süsswasserfauna Deutschlands". Heft 1. Jena.

(24) **Parker, H. W.** (1935). "Reptiles and Amphibians" in "List of British vertebrates". Brit. Mus. (Nat. Hist.). London.

APPENDIX

THE RELATIVE SENSITIVITY OF AQUATIC SPECIES TO LEAD IN SOLUTION

BY J. R. ERICHSEN JONES

The field work of Carpenter (1924*a*, 1925) has established that there is a certain amount of correlation between the lead content of streams and the fauna they support. In slightly polluted waters (3 parts per 10 million) fish are eliminated, but the invertebrate fauna seems to be little affected. As the pollution becomes more serious the Mollusc *Ancylastrum fluviatile* is eliminated, then other Mollusca, Platyhelmia, and Crustacea Malacostraca. With further increase in the lead content Oligochaeta, Trichoptera and Hirudinea disappear, so that the fauna comes to consist of certain adult and larval insects and entomostracan Crustacea only. Finally, in the most highly polluted waters near the mines, containing 3 to 6 parts per million of lead, larvae of the midge *Tanypus nebulosus* and nymphs of the mayfly *Chloëon simile* appear to be the sole survivors.

Attempts have been made to estimate the relative sensitivity of a variety of aquatic species by laboratory experiments. Several series of experiments have shown that the maximum concentration of lead that the stickleback can withstand indefinitely is less than 1 part lead per 10 million of water. Tadpoles (*Rana temporaria temporaria*) are considerably less sensitive, and appear to be unaffected by lead at concentrations below 1 part per million.

The following is a typical experiment: 500 c.c. volumes of solution were employed, in wide mouthed jars and four tadpoles placed in each; four were placed in a similar volume of untreated tap water as controls. The tadpoles were about 20 mm. in length (tail included), they were not fed, and the solutions were not changed. The survival times were as follows:

Concentration (Parts lead per parts water)	Average survival time days
5/1,000,000	1·75
3/1,000,000	5
1/1,000,000	6·75
5/10,000,000	11·75
Controls	9

Thus a concentration of 1 part per million appears to have a lethal effect. No lethal effect was ever observed at concentrations lower. Increase of solution volume produced no change in the general result. Tadpoles of smaller size appeared to be slightly more sensitive, those larger, slightly more resistant.

It was not found possible to determine, in this way, the critical concentration for a large variety of aquatic species; but it is not unreasonable to suppose that the relative sensitivity of a variety of species will be to some extent

Table 4. *Approximate average survival times in lead nitrate solution (Three parts lead per million of water)*

*p*H of solution 6·4

Species		Average survival time	Average survival time of controls days
Limnaea pereger Müll.	A	4 hr.	About 30
Gasterosteus aculeatus L.	A	12 ,,	,, 25
Ancylastrum fluviatile Müll.	B	15 ,,	,, 5
Simocephalus sp.	A	2 days	,, 3
Cyclops sp.	A	3 ,,	,, 3
Simulium sp.	B	4 ,,	,, 7
**Rana temporaria temporaria* L. (tadpoles)	B	5 ,,	,, 9
Sphaerium corneum L.	A	5·3 ,,	Over 70
Chironomus sp.	B	5·4 ,,	,,
Triturus vulgaris vulgaris L. (young with external gills)	A	6 ,,	,,
Chloëon simile Eat.	B	6 ,,	,,
Tubifex tubifex Müll. (small colony with mud)	—	7–10 ,,	,,
Corixa geoffroyi Leach	A	14 ,,	,,
Velia currens Fab.	A	17 ,,	,,
Agrion sp.	B	17 ,,	,,
**Haemopis sanguisuga* L.	A	18 ,,	,,
Anguilla anguilla L.	A	21 ,,	,,
Larval Dytiscidae	B	27 ,,	,,
Planaria vitta Dugès	B	40 ,,	,,
Agabus bipustulatus L.	A	40 ,,	,,
Dytiscus marginalis L.	A	49 ,,	,,
Hydroporus palustris L.	A	50 ,,	,,
Notonecta glauca L.	A	70 ,,	,,
Polycelis nigra Ehrenb.	B	70 ,,	,,

The experiment was discontinued after 70 days, all the animals in the solutions having died. In the case of each species in which the average survival time of controls is given as over 70 days the majority of these were alive at the end of the experiment.

In all cases, except those marked with an asterisk, the survival times are means of six experiments, i.e. six individuals of each species were placed in the solution and six in tap water, as controls. In the cases marked with an asterisk the survival times are means of four experiments.

A, 1000 c.c. of solution not changed throughout experiment. B, 50 c.c. of solution in uncovered Petri-dish renewed daily.

indicated by their relative survival times in a lead solution of a concentration similar to that of the polluted streamlets. Accordingly, using lead solution of concentration 3/1,000,000 (that found in heavily polluted waters near the mines), a series of survival time determinations was made. These are given in order of increasing survival time in Table 4. Survival times of controls are also given, and it will be seen that the result is somewhat complicated by the fact that a number of the species only exist for a limited time in the control water, though in some of such cases (e.g. *Ancylastrum*) the difference in survival time between the animals in the lead solution and the controls is quite significant. Where this complication does not arise, and the controls live indefinitely, the series compares moderately well with the field observations of Carpenter, with

certain notable exceptions, of which the most conspicuous are the Planarians, *Planaria vitta*, and *Polycelis nigra*. No Trichoptera were included in the experiments: Carpenter's field observations indicate that their degree of resistance is of the same order as that of oligochaetes and leeches. It will be observed that the eel is considerably more resistant than the stickleback, and that, of the Invertebrata, the Mollusca are decidedly the most sensitive, while the insects, especially the species breathing atmospheric oxygen, are the most resistant. *Notonecta glauca* survived 25 days in a lead solution of concentration as high as 50 parts per million, and in one experiment a number of large larvae of *Dytiscus marginalis* were kept for 5 weeks in a 20/1,000,000 solution, feeding voraciously on tadpoles during the whole period. After this time they pupated, but none metamorphosed successfully.

NOTES ON THE BIOLOGY OF THE FAEROE MOUSE (*MUS MUSCULUS FAEROENSIS*)

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(*With Plate* 11 *and* 1 *Figure in the Text*)

1. Introduction

Under the auspices of the Oxford University Exploration Club an expedition visited the Faeroe Islands during the summer of 1937. One of the objectives was a study of the Faeroe mouse, and the resulting material is offered in this paper. Collecting apparatus included 48 live traps of the Tring type (**4**) and a number of "break-back" traps; these, however, were not very successful, as they were continually being disturbed by puffins (*Fratercula arctica*). The majority of the mice were caught in simple native traps—small wooden boxes with a trigger and falling door. A total of 48 specimens was secured (14 living and 34 dead) of which 19 were males and 29 females. All the dead specimens were measured; the skins and skulls of 23 have been deposited with the Bureau of Animal Population in Oxford. The living mice were brought back to the Zoological Society of London and to the Bureau of Animal Population.

We should like very much to thank the following for assistance: Mr Charles Elton and the Bureau of Animal Population; the British Museum and the Zoological Society of London; Prof. R. Spärck and Dr Magnus Degerbøl of the Zoologiske Museum in Copenhagen and Dr F. Fraser Darling for personal communications; and the people of the Faeroes who helped us to secure the specimens.

2. Historical

The first known record of mice in the Faeroe Islands is that of Debes (**6**), which dates back to 1673. Landt (**13**), who lived in the islands from 1792 to 1798, reported the mice as being displaced by the rat. As the islands have been inhabited for over 1000 years, it is difficult to say how long the mice may have been there, but by Landt's time they were sufficiently well known to form part of the legend and folklore of the natives. The Faeroe mouse was first described and named in 1904 by Eagle Clarke (**5**) from five specimens obtained on Nolsö by Annandale & Marshall (**1**) in the preceding year. The type is to be found in the Royal Scottish Museum in Edinburgh. It was originally described as a subspecies, *Mus musculus faeroensis* Clarke, and was so considered by Millais (**14**) and Trouessart (**17**); but Miller (**15**) has given it the status of a full

species. Following this lead, Barrett-Hamilton & Hinton (**3**) refer to it as such, "pending further research".

3. Distribution

The Faeroe Islands (Fig. 1) can be divided into three groups: north-eastern, central and southern. A letter from Prof. Spärck of Copenhagen indicates that

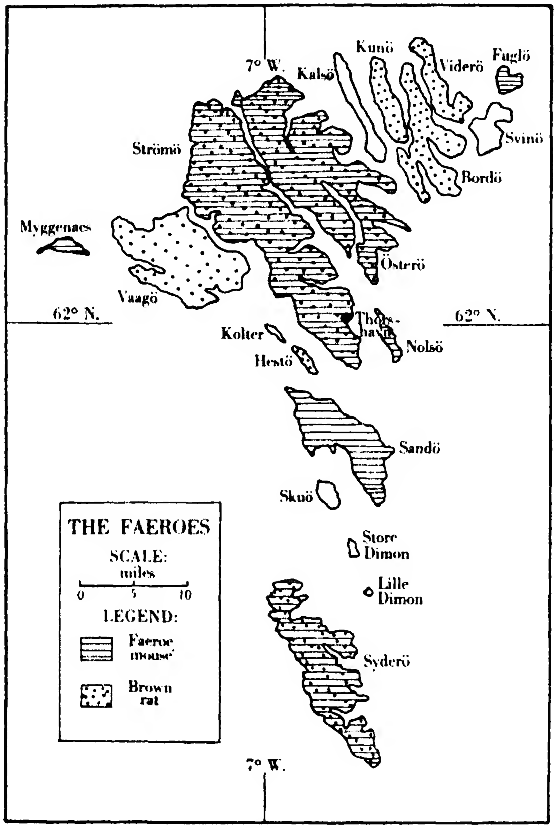


Fig. 1.

mice are found in each group, i.e. on the following islands: Fuglö in the north-east; Myggenaes, Strömö, Österö and Nolsö in the central group; and Sandö and Syderö in the south.[1] With the exception of Syderö, which we did not visit, our observations substantiate this. Prof. Spärck's letter also gives the distribution of the brown rat (*Rattus norvegicus*), which differs strikingly as follows: Viderö, Kunö and Bordö in the north-east; Vaagö, Strömö and Österö in the central group; Hestö and Syderö in the south. We could find no traces of the black rat (***Rattus rattus***), a common species in Landt's time.

The Faeroes are important geographically as the outermost connecting link between Europe and Iceland. Such importance is perhaps minimized in the case of the mice, which are carried by human agencies. Most of the boats put

[1] During recent years mice have appeared in the houses on Hestö (information received Aug. 1938).

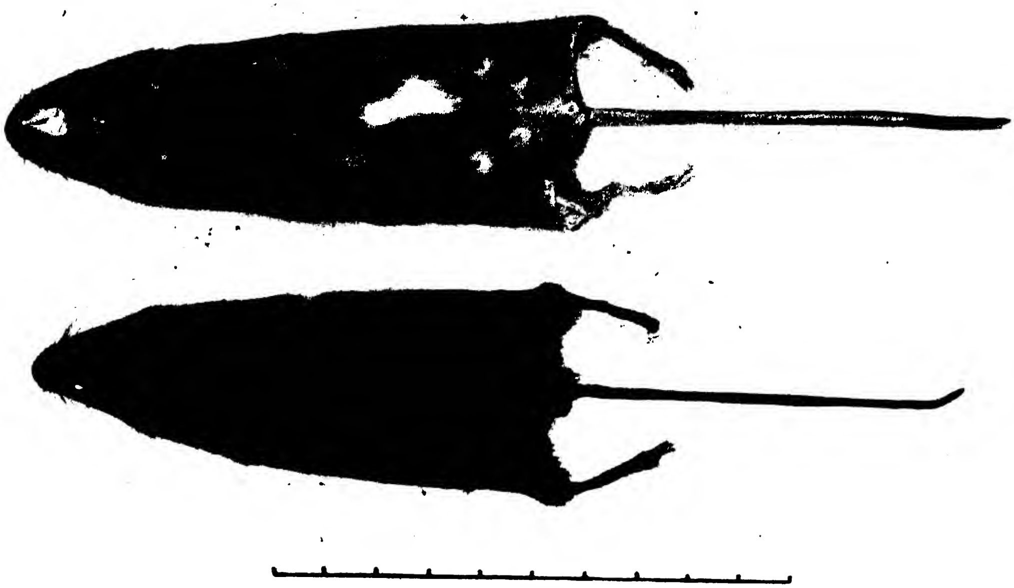
into the Faeroes on their way to and from Iceland. Miller has recorded a series of *Mus musculus* from Reykjavik. The islands do not boast of many good harbours, and the calls made by vessels are few though fairly regular. There is considerable communication among the separate islands, but this is largely by small boats which in many cases cannot dock at all. Myggenaes and Fuglö, with their great cliffs on all sides, are typical of the majority of the islands. The opportunity for isolation to have effect is a good one, in view of the fact that the Faeroe mouse has been there for at least 250 years. A comparable case covering a much shorter period of time is recorded by Jameson (**11**).

4. Forms and status

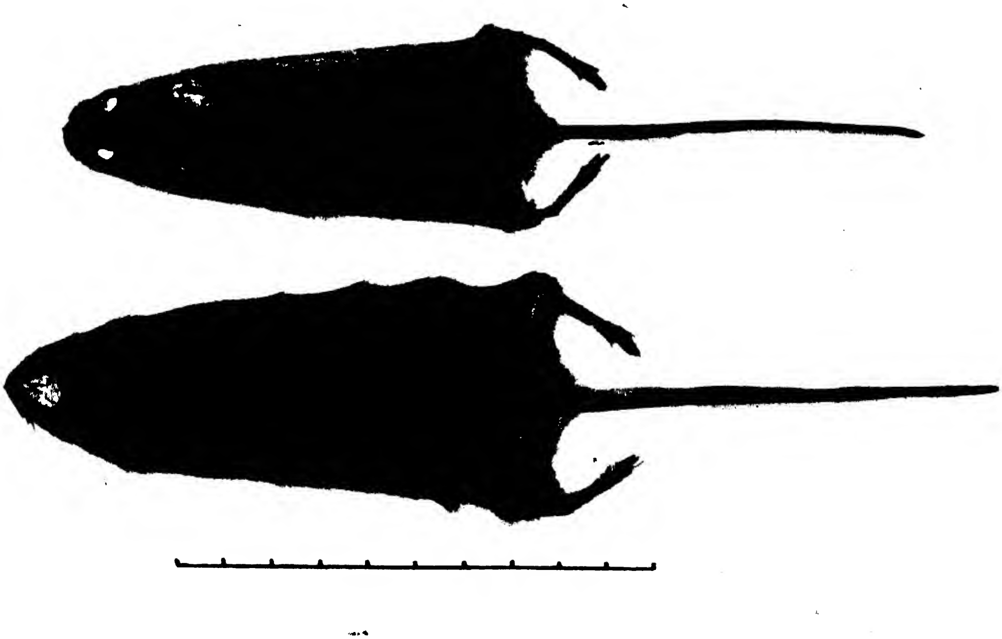
(*a*) *Forms*. The question arises as to whether there is more than one form of mouse in the Faeroes, i.e. are the mice from the cliffs and the fields the same as those in the villages? The islanders believe there are two forms. One of us examined the Faeroe mice in the Copenhagen Museum and was impressed with the relatively small size and dark colour of the specimens from Thorshavn, the largest town and the main harbour of the islands. These differences are also noted by Annandale (**1**). It is possible that the population of Thorshavn mice may be replenished with fresh stock arriving on boats. However, there is no evidence of any such difference in our material from the islands.

(*b*) *Mice on Fuglö*. On Fuglö, the easternmost of the islands and the only one of the north-eastern group where mice are found, we collected 27 specimens. Of these 19 were peculiar in possessing an irregular but strikingly conspicuous white patch on the middle of the belly (Pl. 11, phot. 1); otherwise they appeared typical of the Faeroe mouse. This aberration was present in both sexes and was characteristic of both immature and adult pelage. For this reason it would appear to be inherited, and experiments are now in process to determine the genetics of the problem. The Fuglö population of mice is almost completely isolated, a fact which helps to explain the existence of this peculiarity in 70% of the samples collected. What significance for survival value, if any, can be attached to this variation is impossible to say. The suggestion of Ford (**9**), that non-adaptive visible effects of a mutation may be associated with physiological changes or with some other invisible "factor", may well be applicable here. At any rate, here would seem to be further evidence of the effects of isolation.

(*c*) *Status*. Under the present circumstances it is impracticable to determine the proper status of the Faeroe mouse. Miller's treatment of *M. musculus* and its allies is far from satisfactory and has been criticized in a recent paper by Zimmermann (**19**). Miller's conclusions regarding *faeroensis* were drawn from six specimens, which he found to differ "so conspicuously from all other known members of the group that, however recent the animal's origin may have been, there seems no doubt that the form is a distinct species". The only distinguishing characters given are a larger size, and more robust form and skull; there are no peculiarities of form or structure. The colour, originally



Phot. 1. *Mus musculus faeroensis* from Fuglö. Above, female, No. 24, ventral view. Below, female, No. 3, dorsal view. Scale in cm.
N.B. Note clarity of detail obtained by preparation of skins as flat mounts (see Elton **8a**).



Phot. 2. *Mus musculus faeroensis* from Nolsö (type locality). Above, male, No. 30, dorsal view. Below, female, No. 33, ventral view. Scale in cm.

described as rufous and grey-black on the upper surface, buff and pale grey on the belly, is regarded by Miller as closer to that of *M. musculus* than to that of another related island form, the St Kilda mouse, *M. muralis* Barrett-Hamilton (**2**). The tendency towards robustness is reflected in the development of the stout hind feet. Dr Winge of Copenhagen suggests (see Eagle Clarke (**5**)) that this feature is connected with the mouse's activities among the rocks of the bird cliffs, where some of the original specimens were caught. However, both the Faeroe wren and starling show a similar tendency. In determining the proper status of the Faeroe mouse, it will be necessary to consider the significance of geographical isolation and its effect.

5. Ecological discussion

(*a*) *Habitat.* A great effort was made to secure mice from the bird cliffs, but only one of our collection can accurately be said to have come from there. This was found in a sheep hut on the bird cliffs. Several were taken in the cultivated maerkland and in outbuildings bordering the fields, but the majority were caught in houses in the various villages. As the latter were collected by the natives in their own traps, there is no means of obtaining a statistical analysis of the habitats. The difficulties of collecting on the cliffs were admittedly great, and small colonies might well have escaped notice. An extensive search was made for dung and other signs, but on only one occasion was any discovered. Further investigation of this problem is greatly to be desired. However, it is certain that the villages are important centres of the mouse population, a fact not sufficiently stressed by previous workers, who emphasized the cliff habitats.

(*b*) *Habits.* The one locality in which dung was discovered was in the entrance to a puffin burrow on Myggenaes. Thomas (**16**) reports a wild form of *M. musculus* from Portugal living in association with *Apodemus sylvaticus*, and suggests that the house mouse occupies the burrows of the wood mouse. (*Apodemus* is not found on the Faeroes, however.) The puffins form large colonies of subterranean nests on the slopes above the steep cliffs. The mice that live there apparently do so in association with these birds, whose constant coming and going in countless thousands upset many of the traps and made collecting almost impossible. Both the birds and the burrows would provide excellent protection. Whether the mice remain there after the puffins have gone and throughout the winter is impossible to say. The people both affirmed and denied this belief. The climate is temperate enough to allow for survival during the colder periods of the year.

The experience of Fraser Darling with house-mice on the Treshnish Isles, Argyll, seems very relevant here, and with his permission we include the following report:

Lunga of the Treshnish Isles has been uninhabited by human beings for about 80 years. We went there on 25 August 1937, and pitched our tents near the dry stone walls of the old

houses on the north-east corner of the island. Three days later the first house mouse came into the tent and was drowned in a bowl of water. It was indistinguishable, as far as I could see, from the common house mouse of the mainland.

After that, we were much troubled by the mice and we caught 75 by the time we left at the end of November. We moved camp 50 yd. into a brackeny hollow early in October and the mice were at us again in two days. We saw one old and scabby mouse on the shingle at the shore level at the extreme north point of Lunga. This was ¼ mile away from the old houses and 90 ft. lower.

We were impressed by the immediate return of these mice to house habits. They were far cheekier and more inquisitive than *Apodemus* would have been in similar circumstances and they did their best to take up permanent quarters in the tent.

Elton (**7**) also found that Hebridean house mice normally occur out-of-doors, at least during the summer. They are likewise found living wild in America and Australia. Such facts indicate considerable adaptability as a species, doubtless contributing to a wide distribution. At the same time Fraser Darling's report suggests a habitat preference for domestic conditions, which would tend to keep the house mouse in association with man and act as a retarding influence upon the colonization of new territory away from buildings.

(*c*) *Food.* The Faeroe mouse seems to be almost omnivorous. The villages offer a variety of food in the form of refuse, as well as household stores of meat and grain. The situation on the bird cliffs is quite different, however. A stomach analysis of the specimen taken from the sheep-hut on the cliffs revealed bits of feathers. Within the puffin burrows, possible sources of food include eggs, feathers and refuse of the birds, as well as a small insect population, chiefly Coleoptera, our collection of which has been described by Commander Walker (**18**). The dominant grass, *Festuca ovina*, presumably produces a good quantity of seed which is a potential food supply.

(*d*) *Breeding.* Examinations were made of all the dead females. Three of these contained seven embryos each; a fourth specimen contained only two. One of the living females produced two young, but ate them several days later. Of the total number of females nine weighed over 30 g. each, with two records of over 40 g. each. They were all caught between 17 July and 22 August.

The breeding experiments at the Bureau of Animal Population with mice from Fuglö have not yet been successful, as only the island stock is being used. At the Zoological Society of London a female Faeroe mouse was crossed with a male English house mouse, and a litter of four young was born on 5 April 1938.

(*e*) *Parasites.* All the mice were examined for external and internal parasites. A naked eye examination of the internal organs proved negative. Three ectoparasites were recorded, as follows:

On mice from Nolsö, 22–23 *August* 1937

Acarina: E 1. *Pergamasus crassipes* Linn.
E 2. *Haemogamasus michaeli* Oudemans.
Siphonaptera: E 3. *Nosopsyllus* (*Ceratophyllus*) *fasciatus* Bosc.

The latter is the common rat flea and is recorded from the St Kilda mouse by Harrisson & Moy-Thomas (**10**) and from *Mus musculus* in the Isle of Lewis, Outer Hebrides, by Elton (**7**). It was not included in the list of *Siphonaptera* recently published in the Zoology of the Faeroes (**12**). Prof. Spärck informs us

Table I. *Measurements of Faeroe mice*

Locality	Date (1937)	Collector's no.	Wt. (g.) (including any embryos)	Length (mm.) Head and body	Tail	Hind foot	Ear
A. Females							
Myggenaes	26 July	*2a*	41·5	—	—	—	—
Nolsö	21 Aug.	M	Over 40	—	—	—	—
Fuglö (Kirke)	11 ,,	7*	39	98	86	18	15
Nolsö	22 ,,	26*	37·5	93	91	19	15
Fuglö (Kirke)	12 ,,	24*	36	88	84	18	14·5
Sandö (Sand)	5 ,,	E	36	—	—	—	—
Myggenaes	17 July	B†	34	—	—	—	—
Nolsö	22 Aug.	28‡	30·5	97	88	18·5	15
Myggenaes	27 July	2	30	102	86	18	15
Fuglö (Kirke)	12 Aug.	I	28·5	—	—	—	—
Nolsö	24 ,,	33	27	96	88	18·5	14·5
Fuglö (Kirke)	11 ,,	9	26	90	84	20	15
,,	12 ,,	J	24·5	—	—	—	—
,,	11 ,,	8	23	94	85	19	14
,,	12 ,,	22	22·5	92	86	18·5	15·5
,,	12 ,,	H	22·5	—	—	—	—
Sandö (Sand)	5 ,,	F	22	—	—		—
Fuglö (Kirke)	11 ,,	5	21	86	79	18	14
,,	12 ,,	19	21	85	83	17·5	14
,,	12 ,,	23	21	—	—	—	—
,,	11 ,,	3	19	89	77	17·5	14
Nolsö	23 ,,	32	19	84	74	17·5	13
Myggenaes	26 ,,	C	18·5	—	—	—	—
Nolsö	21 ,,	29	11·5	—	—	—	—
Fuglö (Kirke)	11 ,,	12	10·5	63	65	16·5	12·5
,,	12 ,,	17	9·5	69	63	18	13
,,	11 ,,	14	9·5	66	68	18·5	12·5
,,	12 ,,	20	9·0	—	—	—	—
,,	11 ,,	16	6·0	59	52	16	10·5
B. Males							
Myggenaes	19 July	1	32	98	92	19·5	14
Fuglö (Kirke)	11 Aug.	4	26·5	97	?	17	14
,,	11 ,,	6	25	85	84	18	14·5
Sandö (Sand)	5 ,,	D	24	—	—	—	—
,,	5 ,,	G	24	—	—	—	—
Fuglö (Kirke)	12 ,,	L	23	—	—	—	—
Nolsö	22 ,,	31	21·5	83	76	18·5	13·5
,,	22 ,,	27	21	87	87	18·5	14
Myggenaes	15 July	A	20	—	—	—	—
Nolsö	23 Aug.	30	19·5	81	74	18	13
,,	21 ,,	25	16	83	79	18·5	14
Fuglö (Kirke)	12 ,,	21	16	—	—	—	—
,,	12 ,,	K	14·5	—	—	—	—
Nolsö	21 ,,	N	11·5	—	—	—	—
Fuglö (Kirke)	11 ,,	13	10	69	58	18	13
,,	11 ,,	11	9·5	70	64	19	12
,,	11 ,,	15	8·5	72	64	18	12·5
,,	11 ,,	10	8·5	69	66	19	12·5
,,	12 ,,	18	7·0	63·5	64	18	12·5

* Seven embryos. † Gave birth to two young a few days later. ‡ Two embryos.

that only *Pergamasus crassipes* has been found in the islands before, and that none of the three species has been taken on the Faeroe mouse. Elton (**8**) reports *Haemogamasus michaeli* from *Mus musculus* in the Outer Hebrides, as well as *Pergamasus hamatus* Koch, but not *P. crassipes*. We should like to thank Dr Karl Jordan of Tring and Mr R. J. Whittick of the British Museum for these identifications.

6. Summary

1. An expedition to the Faeroe Islands during the summer of 1937 collected 48 specimens of the Faeroe mouse.

2. Mice have existed there for at least 250 years and are to-day widely distributed, though not found on all the islands. The type locality is Nolsö. The distribution of the brown rat differs strikingly, as shown on the map (Fig. 1).

3. There was no indication of two forms, but a variation with a white patch of hairs on the belly was found in Fuglö.

4. The status of the Faeroe mouse is problematical, an important factor being the significance attached to isolation.

5. The Faeroe mouse has been successfully crossed with the English house mouse.

6. The villages appear to be important centres of populations, with the bird cliffs as marginal habitats where there may be an association with the puffins, which merits further investigation.

7. On the bird cliffs possible sources of food include eggs, feathers and refuse of the birds, a small insect population and a quantity of grass seed.

8. An examination for parasites produced two kinds of mites (Acarina) and one species of flea (Siphonaptera), none of which has previously been taken on the Faeroe mouse. Two are new records for the islands.

References

1. **Annandale, N. & Marshall, F. H. A. (1905).** "The Faroes and Iceland." Oxford, pp. 49–51.
2. **Barrett-Hamilton, G. E. H. (1896).** "On wild forms or sub-species of *Mus musculus*." Zoologist, 20: 178–81.
3. **Barrett-Hamilton, G. E. H. & Hinton, M. A. C. (1921).** "A history of British Mammals." Part 20. London.
4. **Chitty, D. (1937).** "A ringing technique for small mammals." J. Anim. Ecol. 6: 36–53.
5. **Clarke, W. Eagle (1904).** "On some forms of *Mus musculus*, Linn., with description of a new subspecies from the Faeroe Islands." Proc. Roy. Phys. Soc. Edinb. 15: 160–7.
6. **Debes, L. J. (1673).** "Faeroae et Faeroa Reserata." Copenhagen.
7. **Elton, C. (1934).** "Metazoan parasites from mice in the Isle of Lewis, Outer Hebrides." Parasitology, 26: 107–11.
8. **Elton, C. (1936).** "Parasites from rodents and shrews in the Outer Hebrides." Ent. Mon. Mag. 72: 31–4.

8a. **Elton, C. (1938).** "A convenient method of mounting and storing the skins of small mammals." J. Mammal. 19: 244–5.

9. **Ford, E. B. (1931).** "Mendelism and evolution." London.

10. **Harrisson, T. H. & Moy-Thomas, J. A. (1933).** "The mice of St Kilda, with especial reference to their prospects of extinction and present status." J. Anim. Ecol. 2: 109–15.

11. **Jameson, H. L. (1898).** "On a probable case of protective coloration in the house-mouse (*Mus musculus*, Linn.)." J. Linn. Soc. (Zool.), 26: 465–73.

12. **Jensen, Ad. S., Lundbeck, W., Mortensen, T. H. & Spärck, R.** (1937). "The zoology of the Faeroes." Vol. 2. Copenhagen.

13. **Landt, G. (1810).** "A description of the Feroe Islands." London.

14. **Millais, J. G. (1905).** "The mammals of Great Britain and Ireland." Vol. 2. London.

15. **Miller, G. S. (1912).** "Catalogue of the mammals of western Europe (Europe exclusive of Russia) in the collection of the British Museum." London.

16. **Thomas, O. (1896).** "On a wild living mouse of the *Mus musculus* group in Portugal." Zoologist, 20: 137–9.

17. **Trouessart, E. L. (1910).** "Faune des mammifères d'Europe. Conspectus Mammalium Europae." Berlin.

18. **Walker, J. J. (1938).** "On the Coleoptera, etc., of the Faroe Islands." Ent. Mon. Mag. 74: 77–82.

19. **Zimmermann, K. (1935).** "Zur Kenntnis von *Mus musculus* L." Z. Säugetierk. 10: 155–8.

A CENSUS OF BREEDING GANNETS (*SULA BASSANA*) ON MYGGENAES HOLM, FAEROES[1]

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(*With Plate* 12 *and* 1 *Figure in the Text*)

1. Introduction

The earliest reference to the gannet (*Sula bassana* L.) in the Faeroes occurs in the medieval Faeroese ballad "Fuglakvaeði" (**5**), where it is mentioned with a number of other birds, most of which are still common in the islands. This source does not record any breeding place, and at the present time gannets only nest on the holm which lies to the west of the island of Myggenaes, and on the neighbouring stacks, Píkarsdrangur and Flatidrangur. The early works of Debes (**3**), Svabo (**12**), and Landt (**8**) record the position of the colony, but unfortunately do not give any indication of the number of breeding pairs. Landt (1800), probably following Svabo, gives the number of adults killed in April as 200; and the same number of young birds was caught in September. Müller (**9**), writing 62 years later, says that the number of adults and young taken annually was 300 and 600 respectively. Feilden (**4**) visited Myggenaes in 1872, but was unable to cross to the Holm, and Barrington (**2**) in 1892 "estimated the Myggenaes Gannets at 1500", i.e. 750 pairs. Hagerup (**7**) gives photographs but no estimate. Wynne-Edwards, Lockley & Salmon (1936) (**16**) base their figure of 750 breeding pairs on an estimate by Miss Acland (**1**) in 1928, and on the observations of Lockley, who passed close to the colony in June 1935, and estimated that not more than 1000 birds were present.

Salomonsen (**10**) gives no estimate of the total breeding population, but records the number of birds caught annually in recent years as about 450 adults and 850 young. During a visit to Myggenaes in July 1937, the present writers were told by some of the bird-catchers themselves that they only take 600–800 young from the Holm and the two stacks together, of which 150 are caught on Flatidrangur. No adult birds are taken at the present time.

The lack of agreement in these various observations made it desirable to re-examine the status of the Myggenaes colony.

2. The census

The recent censuses of breeding gannets on Ailsa Craig (**14**) and (**15**) have been carried out almost entirely by direct counts from the tops of the cliffs and from the shore (the alighting method has also been used where convenient). The

[1] Gannet Population Studies, No. 4.

nature of the cliff ledges on Myggenaes Holm does not favour the crowded grouping observed on Ailsa Craig, and it was found that on the Holm itself the majority of the nests were placed along a rather broad ledge running along the northern face of the rock, about 100 ft. above sea-level. The remaining nests were mainly in small groups, either above or below this ledge. On Flatidrangur and Píkarsdrangur the birds nest almost exclusively on the summits, which are respectively 81 and 104 ft. above sea-level.

It was found impracticable, and indeed unnecessary, to use the alighting method on Myggenaes Holm, and the results shown in Table 1 are from direct counts by two independent observers. The nests on the main ledges on the Holm and many of the subsidiary groupings were counted from various positions along the tops of the north and west cliffs. The colonies on Flatidrangur and Píkarsdrangur were counted from the pasture land at the south-west corner of the Holm. In a subsequent boat journey round both the Holm and the island, it was possible to include the numbers of the remaining groups on the northern cliffs, and also to reach the summit of Flatidrangur, where the nests were counted at close quarters.

During the last few years there has been a slight spread of the colony on the island of Myggenaes itself. In 1936 and 1937 a single pair of gannets nested on the most westerly point of the island and in both cases a young bird was reared. It should be emphasized, however, that this nest is in full sight of and quite near to the main colony on the Holm, and should in no way be considered as a daughter colony.

The sketch-map (Fig. 1) shows the division of the colony into artificial groups for convenience in counting.

Table 1

	Number of nests	
On Myggenaes	F.C.E.	H.G.V.
On west end	1	1
On Myggenaes Holm		
A	119	120
B	209	209
C	257	250
D	28	28
E	192, 182 } 187	186, 184 } 185
F	211	217
G	224	218
H	35	35
On Píkarsdrangur	122, 118 } 120	116, 110 } 113
On Flatidrangur (count at very close quarters)	232	232
Totals	1623	1608

These figures therefore give the mean number of nests as 1615·5, from which it is concluded that the breeding population of gannets in 1937 was about 3230.

No attempt was made to count the non-breeding birds, which were particularly numerous on some of the main ledges and on part of Flatidrangur.

3. Discussion

From the point of view of population fluctuations the chief interest in the Myggenaes colony lies in the fact that it is one of the few remaining gannetries where birds are captured annually. The number taken rose from 400 in the year 1800, to 900 in 1862, and is now about 600–800. Gurney (**6**) has suggested that the rise in numbers taken in Müller's time (1862) may have been due to "better appliances and greater skill". There seems, however, to be little ground for this suggestion, since the Faeroese fowling

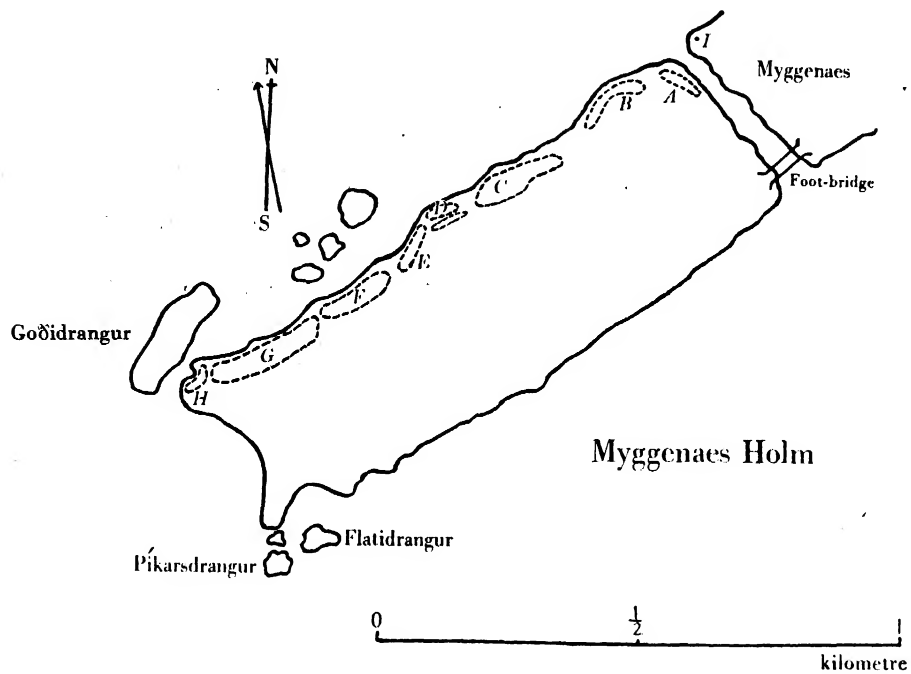

Fig. 1. Sketch-map of Myggenaes Holm (based on the Danish Geodetic Survey).

methods have remained unchanged for centuries. Landt's description (**8**) of the capture of young and adult birds towards the end of the eighteenth century applies almost without modification at the present time.

It may be argued that with the increase in the human population of Myggenaes from 75 in 1801, to 179 in 1925 (**13**), there would be a strong tendency towards an increase in the number of birds taken annually. There are, however, two points against such an argument: (1) as the nesting sites of the gannets are very inaccessible, it would be much simpler to increase the food supply, if it were necessary, by the comparatively easy method of puffin-catching on the bird slopes of Myggenaes itself. It is, indeed, most unlikely that the gannet has ever played a major role in the sea-bird diet of the people of

Photo F. C. Evans

Phot. 1. Flatidrangur and Píkarsdrangur, the two stacks at the west end of Myggenaes.

Photo H. G. Vevers

Phot. 2. Gannets on the summit of Flatidrangur, with the peak of Píkarsdrangur in the right background.

VEVERS and EVANS—Faeroe Gannets

Myggenaes, and nowadays the catch is mainly carried out for "sporting" motives. (2) It is characteristic of the Faeroese fowling methods that great care is taken to guard against any measure of exploitation, which might lead to extermination. It may safely be said that the annual catch would not increase unless a general rise in numbers had been noticed by the fowlers. This may be contrasted with the indiscriminate capture of nestling gannets on Sula Sgeir by men from the Butt of Lewis, in Scotland (**11**).

These facts would suggest that the great increase in the annual capture is an index of increase of the colony as a whole, coincident with the spread of the gannet's breeding range (for example, the new colonies in Shetland), and with a probable increase in the world population of gannets during the last 50 years.

4. Acknowledgements

Our thanks are due to Herr Olaf Heinesen, Herr Pauli Hansen and Herr Abraham Abrahamsen for their assistance on Myggenaes, to Herr Mikkjal Dánjalsson á Ryggi of Bö, in Vaagö, for advice on a number of points, and to Prof. E. S. Goodrich for reading and criticizing the manuscript.

5. Summary

1. Previous records of the Myggenaes gannet colony are reviewed, and an increase in the annual capture during the last 200 years is noted.

2. Details of a census of the whole colony by direct counting are given. From this count it is concluded that the breeding population of gannets in 1937 was 3230.

3. The increase in the annual number of birds taken is probably not correlated with any possible improvements in fowling technique or with the increase in the human population of Myggenaes, but with an increase in the colony as a whole. This increase coincides with a similar fluctuation in the world population of gannets during the last 50 years.

References

(1) **Acland, C. M. (1930)**. "A naturalist's holiday in the Faroes." Game and Gun, and the Country Estate, 7: 114–18, 166–70.

(2) **Barrington, R. M. (1892)**. Cited by Gurney (**6**), p. 271.

(3) **Debes, L. J. (1673)**. "Faeroae et Faeroa Reserata." Copenhagen.

(4) **Feilden, H. W. (1872)**. "The birds of the Faeroe Islands." Zoologist, 7: 3285.

(5) **Grundtvig, S. & Bloch, J. (1872–6)**. "Føroyja kvaedi. Corpus Carminum Faeroensium. Faerøernes gamle Folkeviser." København. (MS. in Det Kongelige Bibliothek, Copenhagen.)

(6) **Gurney, J. H. (1913)**. "The gannet. A bird with a history." London, p. 270.

(7) **Hagerup, O. (1926)**. "Communities of birds. Oecological studies. 1. The communities of birds of the North Atlantic Ocean." Vidensk. Medd. Dansk Naturh. Foren. Kbh. 82: 127–56.

(8) **Landt, J. (1800)**. "Forsog til en Beskrivelse over Faerøerne." Copenhagen.

(9) **Müller, H. C.** (**1862**). "Faeröernes Fuglefauna med Bemaerkninger om Fuglefangsten." Vidensk. Medd. Dansk. Naturh. Foren. Kbh. p. 73.

(10) **Salomonsen, F.** (**1935**). "Aves", in "Zoology of the Faroes." Copenhagen, p. 254.

(11) **Stewart, M.** (**1938**). "Notes on the gannetries of Sule Stack and Sula Sgeir." British Birds, 31: 282–94.

(12) **Svabo, J. C.** (**1782**). MS. quoted by Feilden (**4**).

(13) **Trap, J. P.** (**n.d.**). "Faerø Amt." Extract from "Kongeriget Danmark". 4th ed. Copenhagen.

(14) **Vevers, H. G. & Fisher, J.** (**1936**). "A census of gannets on Ailsa Craig, with a new method of estimating breeding-cliff populations." J. Anim. Ecol. 5: 246–51.

(15) **Vevers, H. G., Fisher, J., Hartley, C. H. & Best, A. T.** (**1937**). "The 1937 census of gannets on Ailsa Craig; with notes on their diurnal activity." J. Anim. Ecol. 6: 362–5.

(16) **Wynne Edwards, V. C., Lockley, R. M. & Salmon, H. M.** (**1936**). "The distribution and numbers of breeding gannets (*Sula bassana* L.)." British Birds, 29: 262–76.

THE 1938 CENSUS OF GANNETS (*SULA BASSANA*) ON AILSA CRAIG

By H. G. VEVERS and JAMES FISHER

In 1936 (**1**) and 1937 (**2**) censuses of gannets (*Sula bassana* L.) were made on Ailsa Craig, in the former year by means of direct counts, and in 1937 by direct counts and the alighting method. The present census was made by direct counts alone.

The natural and artificial groupings used in the former years have been retained, for the most part without the necessity for any change. We have, however, to add a new group of some 25 nests, situated directly above the "Main Craigs East" (see diagram in **2**). The census was made between 5 and 12 April. The complete results are shown in the following table:

Table 1

Cliff	1938 direct counts: Counts (pairs)	1938 direct counts: Mean	Increase or decrease (compared with 1937)
Barestack	95, 97	96	[illegible]
Northwards of Ashydoo	287, 293	290	–
Ashydoo A 1	189, 188, 197, 184	189·5	+
,, A 2	32, 32, 33, 34	32·75	–
Balvaar	522, 539	530·5	[illegible]
Balvaar-Cairn	58, 60, 60	59·33	–
Cairn	606	606	–
Barrheads, S.	38	38	–
,, Mid	19	19	+
,, N.	95	95	+
Cairn-Mare and part of N. Barrheads	452	452	+
Mare	1684, 1692	1688	–
Mare-Stranny Point:			
S 1	82, 80, 82	81·33	
S 2	65, 53, 56, 64, 64	60·4	–
S 3	108, 115, 123	115·33	–
S 4	191, 180	185·5	–
Main Craigs:			
Top	276, 268	272	+
Main Part	403, 404, 400, 398	401·25	+
East	107, 109, 99, 104, 99, 109	104·5	+
Far East	47, 47, 45, 47, 43	45·8	+
East Top (new)	23, 26	24·5	+
	Total = 5387 pairs (approx.)		

The total number of breeding pairs in 1937 was 5945. There has therefore been a decrease of 9·4% (approximately) over the colony as a whole. Among the individual groups of nests the only significant decrease has taken place in the Mare and Cairn. In contrast to this there has been an increase of all the groups on the Main Craigs.

Observations have been continued on the diurnal activity of the gannets, but we are awaiting further evidence before publication.

We are extremely grateful to L. S. V. Venables, Malcolm Stewart and L. P. Madge for their assistance in making counts, and especially for their constructive criticism of census methods. This has resulted in a slight revision of our ideas as to the efficacy and reliability of the alighting method, and we hope to make further and fuller analyses of it.

REFERENCES

(1) **Vevers, H. G. & Fisher, J. (1936).** "A census of gannets on Ailsa Craig, with a new method of estimating breeding-cliff populations." J. Anim. Ecol. 5: 246–51.

(2) **Vevers, H. G., Fisher, J., Hartley, C. H. & Best, A. T. (1937).** "The 1937 census of gannets on Ailsa Craig; with notes on their diurnal activity." J. Anim. Ecol. 6: 362–5.

GANNETS (*SULA BASSANA*) ON NOSS, SHETLAND, WITH AN ANALYSIS OF THE RATE OF INCREASE OF THIS SPECIES[1]

By JAMES FISHER and L. S. V. VENABLES

(*With Plate* 13 *and* 2 *Figures in the Text*)

1. Previous counts and estimate

Gannets (*Sula bassana* L.) showed interest in the Noup of Noss in 1911 or 1912, Mr G. T. Kay tells us (**18**), and the colony was established in 1914, when one pair is reported by MacPherson (**21**) as having bred. In the following year four pairs bred (**29**). In 1918 three young were reared, and in 1919 there were five pairs (**12**) and in 1920 10 (**35**). In 1930 or 1931 Mr George Russell (**25**) estimated about 200 pairs.

In the world estimate of the numbers of breeding gannets undertaken by Wynne-Edwards, Lockley & Salmon (**8**), the numbers of gannets on Noss in 1934 and 1935 were recorded as in the neighbourhood of 800 pairs. The roughness of this estimate (made by L. S. V. V.) was perhaps not sufficiently stressed by the writers. It was based on the combination of a count of the number of incubating pairs on a control area of cliff, and an estimate of the total density by comparison.

2. Description of the colony

In their paper Wynne-Edwards, Lockley & Salmon gave the impression that "Noss" and the "Noup" were two distinct breeding-cliffs. In fact the Noup is the great cliff, rising to 600 ft. above sea-level, which forms the eastern side of the island of Noss. The cliffs of Noss (Fig. 1) can be divided topographically into three parts, the North (A) and South (B) faces of the Noup, and Rumble Wick (C), the cliff between the Noup and Geordie's Holes, a point above the Holm of Noss. The Holm is a stack on which breeds a colony of over 200 pairs of great black-backed gulls (*Larus marinus*).

On (C) is an excellent stance from which part of the gannet colony can be closely watched, and which alone gives an uninterrupted view of all the inhabitants of one of the large ledges (X). The whole faces of the cliffs (A), (B) and (C) can be viewed from a distance, (B) from (C), and vice versa, and (A) from a shoulder of cliff, the Point of Heogatoug, north of the Noup.

[1] Gannet Population Studies, No. 5.

3. 1937 Estimate and 1938 Count

1937. We visited Noss on 27 and 29 August 1937, before any young gannets had left the nest. On 27 we made a trial, and on 29 a final estimate of the numbers of breeding pairs by the alighting method (**32**).

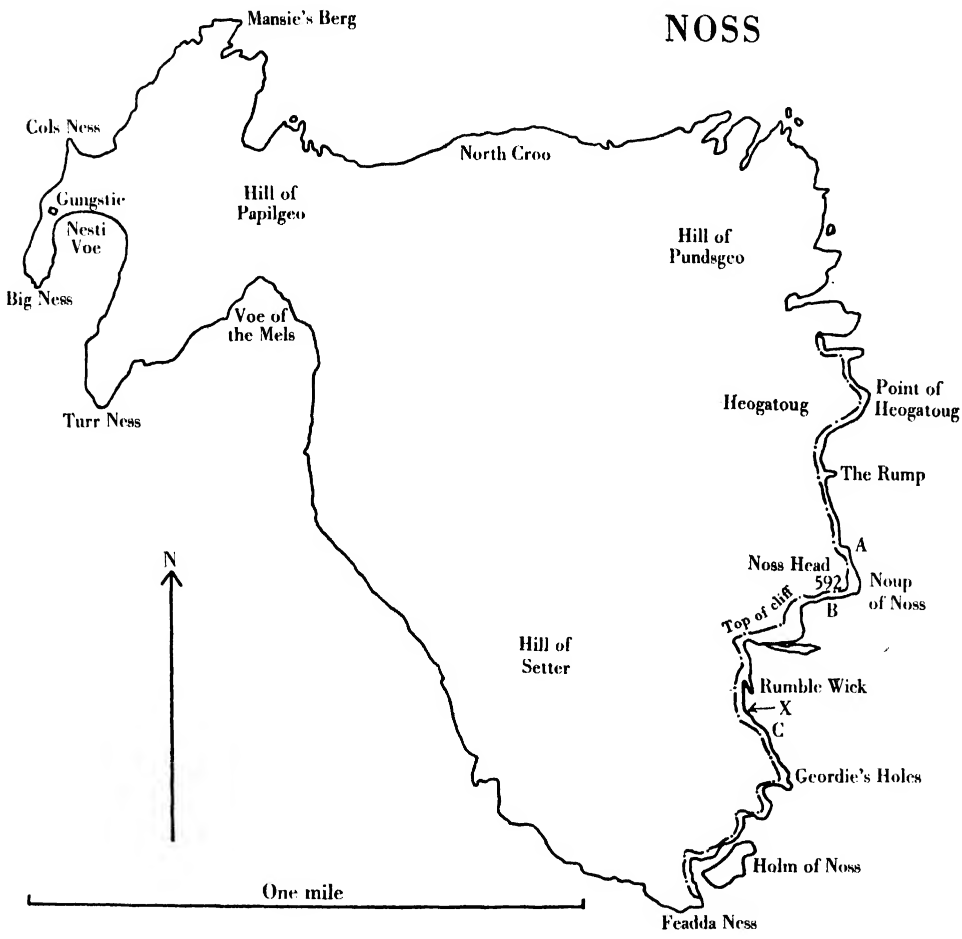

Fig. 1. Sketch-map of Noss, Shetland. (Based upon the Ordnance Survey map with the sanction of the Controller of H.M. Stationery Office.)

We decided to use the ledge (X) as our control group. Five separate counts (by three observers, D. Lack, J. F. and L. S. V. V.) of the number of pairs gave 67, 67, 68, 69, 69: mean 68.

29 August was a calm day and throughout the afternoon there was no change of wind. We first counted the number of birds that alighted on (X) in 30 min., then on (A), (B) and (C) separately in 10 min., then on (X) for a

Phot. 1. The Noup of Noss, from Rumble Wick. *Photo J. Fisher*

Phot. 2. Part of the control area X in June 1935. *Photo L. S. V. Venables*

further 30 min. thus tending to correct any change in activity of the whole colony over the intervening period. Our results were:

On (X)	46	alighted in	30	min.	
(A)	111	,,	10	,,	
(B)	53	,,	10	,,	
(C)	71	,,	10	,,	
(X)	59	,,	30	,,	(2nd count)

i.e. total alighting on (A), (B) and (C) in 10 min. = 235, and mean alighting on (X) in 10 min. = 17·5, which gives as an estimate for the total number of breeding pairs 68 × 235/17·5 = 913 (to nearest pair).

We cannot claim very great accuracy for this method. Vevers & Fisher (**32**) claimed great accuracy in their original description of the method as used on Ailsa Craig. But as they remark elsewhere (**33**), further studies have meant a revision of their claims, and the figure 913 may involve an error of 20% or more.

1938. In this year we were able to devote the days 22 June to 4 July to the gannets, and found that it was possible, with the aid of powerful glasses, to make direct counts of the number of nests. With the kind help of Malcolm Stewart and the co-operation of Mr G. T. Kay, we obtained the following results:

		J.F. 22.vi.38	J.F. 30.vi.38	L.S.V.V. 30.vi.38	M.S. 3.vii.38	M.S. 4.vii.38	Total taken as
A. N. face of Noup (from Point of Heogatoug)		463	480	458	438	—	460
Add dead ground, counted from boat		35	—	—	—	—	35
B. S. face of Noup (from Rumble Wick)	Group 1	—	212, 212	221	241	—	222
	2	—	61	63	57	—	60
C. Rumble Wick (from Noup)	Group 1	109	116	120	106	—	113
	2	292	315	295	296	—	300
	3	—	150, 168	145, 156	152*	176	159
	4	—	171	170	137*	165	169
						Total	1518 nests

* Omitted, owing to mist and the presence of a naval boat letting off rockets.

We consider this count to be much more accurate than the 1937 estimate.

4. Relations with other birds

Gannets compete for nesting sites with only one bird, the guillemot, *Uria aalge* (Pontopp.), since the other cliff-breeders do not use broad ledges on Noss. Guillemots still try to return to the ledges which the growing numbers of gannets have colonized. On these ledges the gannets have "beak-range" territories, between which guillemots may succeed in laying their egg. If the egg should roll within beak range of a gannet it can never be recovered by the guillemot, and in June many can be seen abandoned. This factor is probably of some importance in affecting the number of guillemots on a cliff where gannets are increasing.

On Noss 50 pairs of great skuas, *Stercorarius skua skua* (Brunn.), bred in 1932, 67–70 bred in 1934 (**30**). In 1937, according to the estimate of J. W. Jamieson (**17**), the R.S.P.B. watcher, they had again increased and in 1938 L. S. V. V. counted c. 80 pairs. These birds pursue gannets and make them throw up their fish, but it is impossible to say whether they seriously affect the food supply to the young. They have never been seen to kill an adult or young gannet.

5. Mortality of young

On the control ledge (X) 68 pairs of gannets had 57 chicks on 29 August 1937, which could be expected to fly in from one to three weeks. Since the cliffs fall sheer into the sea, and there is no beach of any kind, mortality cannot be examined at the cliff-foot as on Ailsa Craig and other gannetries.

6. Colonization

Obviously the Noss gannetry and its history brings up the question raised by Ingram & Salmon (**16**) over the Grassholm gannetry. The question arises, is the increase of gannets on Noss due entirely to colonization, or can it be accounted for, after the first few years, by the natural increase of the gannet when undisturbed and protected?

What can the natural increase of the gannet be? We must first find out three things: (*a*) the age at which gannets can breed, (*b*) how many years the "average" gannet will continue to breed, and (*c*) the sex ratio.

(*a*) It is generally held that gannets hatched in year n can breed in year $n+4$, though it has been suggested that they can breed in year $n+3$. Gurney (**13**) rather avoided the question in his book. Booth (**6**) is the only man to have bred the gannet in captivity. He obtained from the Bass Rock:

In 1874, 4 fledglings,
In 1875, 2 ,,
In 1876, 2 ,, .

In 1879 a pair began to build, and he states that "after sitting five or six days the *young birds* [our italics] succeeded in dragging away some of the materials and smashed the egg. The nest was reconstructed immediately; but though the bird continued sitting for several days, it was eventually deserted." In 1880 and 1881 the same pair brought young off successfully. It is clear, then, that the pair which tried to breed in 1879 came from the Bass Rock as fledglings in 1874 or 1875, and bred when the 1876 pair were still "young". This points to $n+4$ (or $n+5$) breeding, and provides some evidence for ruling out $n+3$. Booth's study of plumage changes (supported by pictures) also seems to show that full plumage is not attained until at least $n+4$. We are therefore supposing that a gannet hatched in the year n can breed in the year $n+4$.

(*b*) There is very little evidence on the longevity of gannets. Records from captive birds in zoos (**9, 10**) give us (London) 12 years, 9 months, 27 days; and

6 years, 1 month; (Copenhagen) two birds about 13 years. The mean length of life of the eight longest-lived in captivity, mostly caught as adults, is about $8\frac{1}{2}$ years. On the other hand, the closely related pelicans may live in captivity up to 51 years. Evidence from ringing returns is scanty and cannot yet be expected to give a satisfactory contribution to this problem; with the exception of a private scheme in 1904 (**28**) ringing of gannets has only seriously been carried out since 1913 (**36**). The longest lived ringed gannet recovered so far was marked on Ailsa Craig as a nestling on 30 July 1924 and recovered near the Craig on 1 April 1932 (**3**). Maynard (**22**) dissected a female gannet "with the ovaries nearly depleted, there being about a hundred and forty ruptured capsules, among which are interspersed a comparatively few ovules. As a ruptured capsule indicates most surely that an egg has been deposited, it is reasonable to suppose that this gannet has laid something like one hundred and forty eggs and, as there is but one egg normally laid in a season, this would give an approximate great age to the bird, even if we allow for occasional accident to an egg, when a second specimen would be deposited that season."

(*c*) Gannets appear to be strictly monogamous birds; amongst a mass of negative evidence for this, we must adduce the positive fact of their very rigid type of mutual courtship. Therefore it would be unsafe to say that if there were more females than males, there would be more chicks per gannet. On the contrary, a sex ratio other than 1 : 1 would tend to lower the potential increase. In the absence of any statistical evidence, we are *assuming* that the sex ratio is actually 1 : 1.

The argument that follows is put forward after consultation with Prof. J. B. S. Haldane (**14**), and the writers are very grateful to him for his assistance with this biometric problem. C. F. Fisher has also given useful help.

Suppose there are p_n pairs of gannets in the year n, aged 4 years and over, and that each produces 1 chick, the sex-ratio being 1 : 1. The maximum rate of increase is given if all birds are immortal and perpetually fertile. In this case the number in each year, provided no colonization takes place from outside, is increased by half the number of birds hatched 4 years earlier, i.e. by $\frac{1}{2}p_{n-3}$.

Thus if $n=1936$, $$p_{1937}=p_{1936}+\tfrac{1}{2}p_{1933}.$$

In general, $$p_{n+1}=p_n+\tfrac{1}{2}p_{n-3},$$

or $$p_{n+4}-p_{n+3}-\tfrac{1}{2}p_n=0. \qquad \ldots\ldots(1)$$

Hence, in the long run, values of p_n will tend to a geometrical progression whose common ratio is the largest root of

$$x^4-x^3-\tfrac{1}{2}=0, \text{ i.e. } x=1{\cdot}25 \text{ (approximately)},$$

and $$p_{n+m}=1{\cdot}25^m p_n, \text{ or } \log p_{n+m}=\log p_n+m\log 1{\cdot}25.$$

On Grassholm in 1924 (**1**) there were about 2000 pairs of gannets. In 1933 there were about 5500 pairs (**26**). Ingram & Salmon (**16**) calculated that this

increase could be caused by an annual increment of about 10%. The actual annual increase x would be given by the equation

$$\log p_{1933} = 9 \log x + \log p_{1924},$$

i.e.

$$\log 5500 = 9 \log x + \log 2000,$$

and

$$x = 1{\cdot}119 \text{ (approximately)},$$

and the annual increase would be approximately 11·9%.

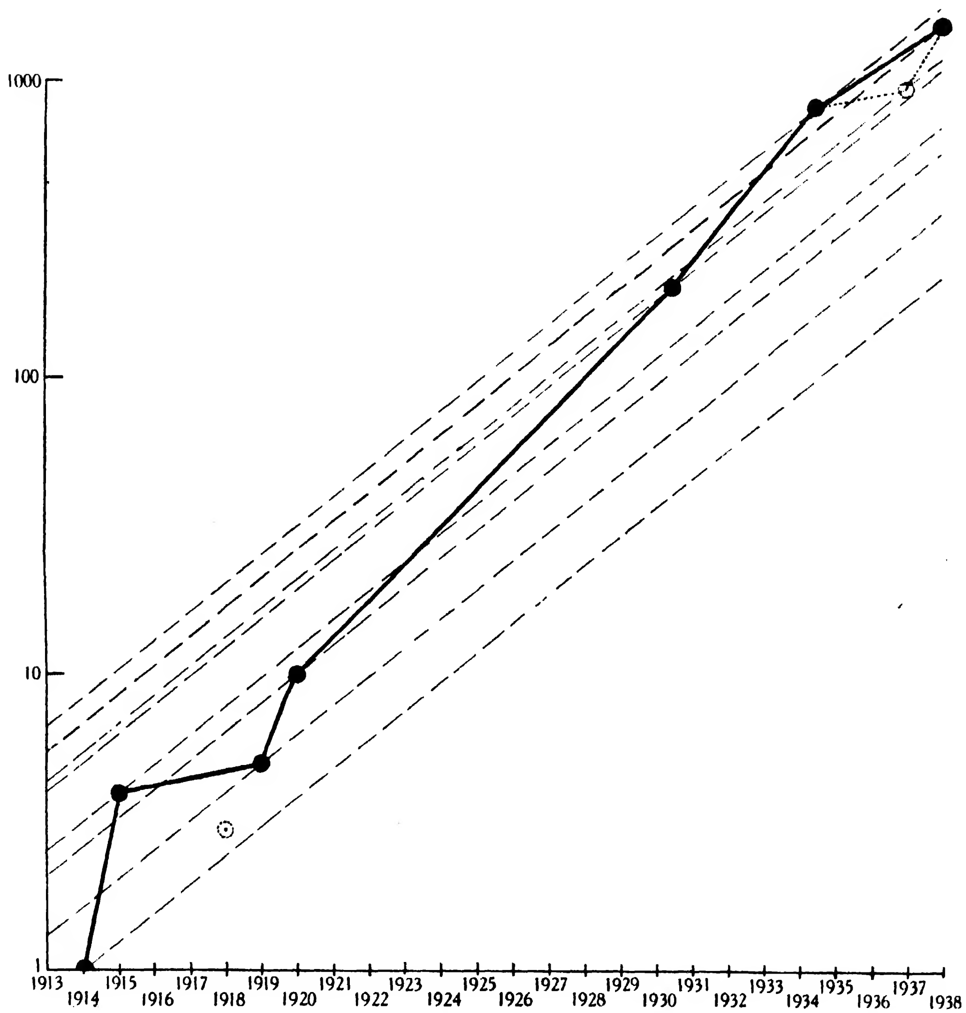

Fig. 2. Increase of gannets on Noss, plotted on arithlog paper. —— actual increase; - - - theoretical increase if there is no colonization, and if all gannets are immortal.

They held, too, that this increase could be accounted for by a survival rate of young equivalent to 30% reaching maturity.

Table 1

Stage of colony	Factors affecting numbers: Promoting	Factors affecting numbers: Limiting
1. Birds interested, and attempts at breeding, e.g. Lundy 1922 (**20**), Isle of May 1922 (**5**), Bempton Cliffs 1924–8 (**24**) and Great Saltee 1929-32 (**23**)	(*a*) Habitat selection Primary, islands Secondary, ledges of right shape and size Tertiary, steep cliff (*b*) General increase in other colonies causing pressure on sites, see (*j*) and emigration	
2. First bird or birds lay eggs. More non-breeders than breeders present, e.g. on Funk Island (**11**), Great Saltee (**23**)	(*c*) Existence of threshold number of birds necessary to provide the required social stimulus to breeding (**5**). A solitary pair can, however, breed, e.g. Horse of Copinsay 1914 (**4**), Noss 1914 (**21**), Great Saltee 1933 (**19**, **23**), and Bempton Cliffs 1937-8 (**6a**)	
3. Colony established and increasing. More breeders than non-breeders	(*d*) Further colonization (*e*) Possibility of greater breeding-efficiency due to social stimulus of increased numbers	
4. Young produced in stage 2, now breeding	(*f*) Element of conservatism now enters. Ringing records show young tend to return to colony of origin. One real exception, bird ringed young Ailsa Craig 19 July 1924 recovered 25 miles N.W. Muckle Flugga, Shetland 9 June 1926 (**2**) (near known colony at Herma Ness)	(*g*) Limits of natural rate of increase (*h*) Mortality 1. In nest 2. In adolescence 3. When adult, which may be due to countless factors including man (**27**, **31**), oiling (**34**), accidents, particularly when landing on cliff, and disease
5. Colony still increasing	(*i*) Plasticity of nest-site selection comes into play. Under pressure from cliff-nesting gannets some will breed on grass and flat ground, e.g. Grassholm (**1**, **26**), which has small cliffs	(*j*) Supply of nest-sites limited (*k*) Quarrying, etc., e.g. Ailsa Craig (**34**), Bull Rock (**13**)
6. Decrease and final extinction. More non-breeders than breeders, e.g. Lundy (**13**)	(*l*) Conservatism so strong that birds will return for many years even if unable to breed, Lundy (**13**) (*m*) Continuance of (*a*)	(*n*) Collectors, e.g. Lundy (**13**) (*o*) Earthquakes, e.g. Grimsey (**15**, **24**) (*p*) Mortality of conservative gannets (*q*) Threshold factor (*c*) now has effect on debit side, but may be overweighed by (*l*) until all is finally lost
7. Recolonization. See (*l*). Examples Funk Island (**11**) after 100 years, Lundy (**20**) attempt after 15	(*r*) See (*a*), etc.	

Supposing, once adult, they were immortal, the actual survival rate y would be given by the equation

$$x^4 - x^3 - \tfrac{1}{2}y = 0,$$

i.e. $$y = 0{\cdot}3334 \text{ (approximately)},$$

and one-third would reach maturity.

7. Conclusions

(*a*) *Special.* We may conclude, from a study of Fig. 2, that the numbers of gannets were small and perhaps unsteady for the first six years, but that afterwards increase took place at a rate greater than is possible in a closed population, even supposing all gannets to be immortal. Colonization from outside has therefore taken place right up to 1934 or 1935. After that it can be seen that the actual rate of increase has fallen below the "immortality rate", and we have no clear evidence for further colonization.

(*b*) *General.* The establishment and history of a colony of sea-birds such as gannets deserves examination in the light of Fraser Darling's recent book (**7**) on bird flocks and the breeding cycle. Let us frame our treatment in the form of Table 1 (p. 311).

8. Summary

1. Gannets (*Sula bassana* L.) on Noss, Shetland, have increased from 1 pair in 1914 to 1518 breeding pairs in 1938.

2. Relations with other birds are discussed.

3. On 29 August 1937 a group of 68 pairs had 57 chicks.

4. Until 1934 or 1935 colonization took place from outside.

5. There is no evidence for colonization after 1935, though it is probable.

6. If gannets were immortal and perpetually fertile, their increase in a closed community would be approximately 25% per annum. In nature, then, an increase more rapid than this *must* be partly due to colonization.

7. If only one-third of young gannets reach maturity, and once mature are immortal, their increase in a closed community will be approximately 12% per annum. In nature an increase more rapid than this is *probably* due to colonization.

8. An increase of under 12% per annum gives no clear evidence for colonization.

9. The effect is discussed of such factors as habitat selection, social breeding stimulus, "conservatism", possible rate of increase, mortality, supply of nest sites, earthquakes, collectors and man on the history and numbers of a gannet colony.

REFERENCES

1. **Acland, C. M. & Salmon, H. M. (1924).** "The Grassholm gannets in 1924—a great increase." Brit. Birds, 18: 178–85.

2. **Anon. (1927).** "Recovery of marked birds." Brit. Birds, 20: 242–50.

3. **Anon. (1932).** "Recovery of marked birds." Brit. Birds, 26: 208–20.

4. **Aplin, O. V. (1915).** "Gannet nesting in Orkney." Zoologist, 19: 433.

5. **Baxter, E. V. & Rintoul, L. J. (1923).** "Report on Scottish ornithology in 1922, including migration." Scot. Nat. 1923: 65–84, 101–22.

6. **Booth, E. T. (1883).** "Rough notes on the birds observed during twenty-five years' shooting and collecting in the British Islands." Vol. 3 (Gannet. *Sula bassana*): 1–15.

6a. **Booth, H. B. (1938).** Personal communication; letter dated 26 June, 1938.

7. **Darling, F. Fraser (1938).** "Bird flocks and the breeding cycle. A contribution to the study of avian sociality." Cambridge.

8. **Edwards, V. C. Wynne, Lockley, R. M. & Salmon, H. M. (1936).** "The distribution and numbers of breeding gannets (*Sula bassana* L.)." Brit. Birds, 29: 262–76.

9. **Flower, S. S. (1926).** "Contributions to our knowledge of the duration of life in vertebrate animals. 4. Birds." Proc. Zool. Soc. Lond., 1925: 1365–422.

10. **Flower, S. S. (1938).** "Further notes on the duration of life in animals, 4. Birds." Proc. Zool. Soc. Lond. Ser. A, 108: 195–235.

11. **Gilliard, E. T. (1937).** "The gannets of Funk Island." Auk, 54: 379–81.

12. **Greatorex, C. (1919).** "Some ornithological notes from Shetland." Brit. Birds, 13: 159–60.

13. **Gurney, J. H. (1913).** "The gannet. A bird with a history." London.

14. **Haldane, J. B. S. (1937).** Personal communication.

15. **Holmes, P. F. & Keith, D. B. (1935).** "The gannet colony of Grimsey, North Iceland." Brit. Birds, 28: 319–20.

16. **Ingram, G. C. S. & Salmon, H. M. (1934).** "Birds in Britain to-day." London.

17. **Jamieson, J. W. (1937).** Personal communication.

18. **Kay, G. T. (1937).** Personal communication.

19. **Kennedy, P. G. (1934).** "Gannets and choughs on Great Saltee Island." Brit. Birds, 27: 362.

20. **Loyd, L. R. W. (1922).** "Observations on the birds of Lundy, May and June." Brit. Birds, 16: 148–59.

21. **MacPherson, A. H. (1933).** "Gannets in Shetland." Scot. Nat. 1933: 118.

22. **Maynard, C. J. (1889).** "Notes on the anatomical structure of three species of gannets." Contributions to Science, 1: 151–3.

23. **Pollard, R. S. (1934).** "Problems of colonization and increase of sea-birds on Great Saltee Island." Brit. Birds, 27: 290–2.

24. **Roberts, B. (1934).** "The gannet colonies of Iceland." Brit. Birds, 28: 100–5.

25. **Russell, G. (1937).** Personal communication.

26. **Salmon, H. M. & Lockley, R. M. (1933).** "The Grassholm gannets—a survey and a census." Brit. Birds, 27: 142–52.

27. **Stewart, M. (1938).** "Notes on the gannetries of Sule Stack and Sula Sgeir." Brit. Birds, 31: 282–94.

28. **Thomson, A. Landsborough (1926).** "Problems of bird-migration." London.

29. **Tulloch, J. S. (1915).** "Nesting of the gannet in Shetland: an extension of its breeding range." Scot. Nat. 1915: 251.

30. **Venables, L. S. V. (1934).** "Census of breeding skuas on Noss." Brit. Birds, 28: 87.

31. **Vevers, H. G. & Evans, F. C. (1938).** "A census of breeding gannets (*Sula bassana*) on Myggenaes Holm, Faeroes." J. Anim. Ecol. 7: 298–302.

32. **Vevers, H. G. & Fisher, J. (1936).** "A census of gannets on Ailsa Craig, with a new method of estimating breeding-cliff populations." J. Anim. Ecol. 5: 246–51.

33. **Vevers, H. G. & Fisher, J. (1938).** "The 1938 census of gannets (*Sula bassana*) on Ailsa Craig." J. Anim. Ecol. 7: 303–4.

34. **Vevers, H. G., Fisher, J., Hartley, C. H. & Best, A. T. (1937).** "The 1937 census of gannets on Ailsa Craig; with notes on their diurnal activity." J. Anim. Ecol. 6: 362–5.

35. **Waldo, E. G. B. Meade- (1920).** "A new nesting-place of the gannet." Brit. Birds, 14: 93–4.

36. **Witherby, H. F. (1917).** "Marked gannet in Northern Norway in winter." Brit. Birds, 11: 22.

THE COMPARATIVE BREEDING ECOLOGY OF TWO SPECIES OF *EUPLECTES* (BISHOP BIRDS) IN USAMBARA

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(With 2 Figures in the Text)

CONTENTS

1. Introduction

Euplectes nigroventris Cassin, the Zanzibar red bishop, and *E.h. hordeacea* (Linn.), the crimson-crowned bishop, are weavers of the subfamily Ploceinae. On the biology of the former species nothing appears to have been recorded hitherto except the notes reproduced by Reichenow (1904) and those of Vaughan (1929), who (rightly) suspected it to be polygamous. For *Euplectes hordeacea* we take the work of Lack (1935) as basis and amplify only certain points. Our study is more incomplete than we should have wished because we could not make continuous observations and because of an unexpected technical difficulty.

The males of both these bishop birds have a highly conspicuous red breeding dress and are at other times practically indistinguishable in the field from females and young. Both are territory-holding species dependent on grasses for their food and their nesting materials. The architecture of their nests, which are similar except in size, demands close upright vegetation. The rather restricted geographical range of *E. nigroventris* is wholly contained in that of *E. hordeacea*. The two species may often be found side by side, but in our experience there is little ecological overlap; the smaller *E. nigroventris*

prefers more swampy conditions than the other bird, and we have not found them both numerous in proximity, although this may occur elsewhere (Fuggles-Couchman *in litt.*). Practically all our observations on *E. nigroventris* have been made at Mkomasi near Buiko, under the western edge of the Usambara Mountains, and those on *E. hordeacea* between Amani and the coast. (For map and general description of the country see Moreau (1935).) Owing to the height of the vegetation in which they usually nest—6–10 ft.—an elevated viewpoint is necessary for working out the territories of both species; of the two, *E. hordeacea* is much the more difficult to obtain nesting data for, because the vegetation it prefers is exceedingly tall, dense and bristly.

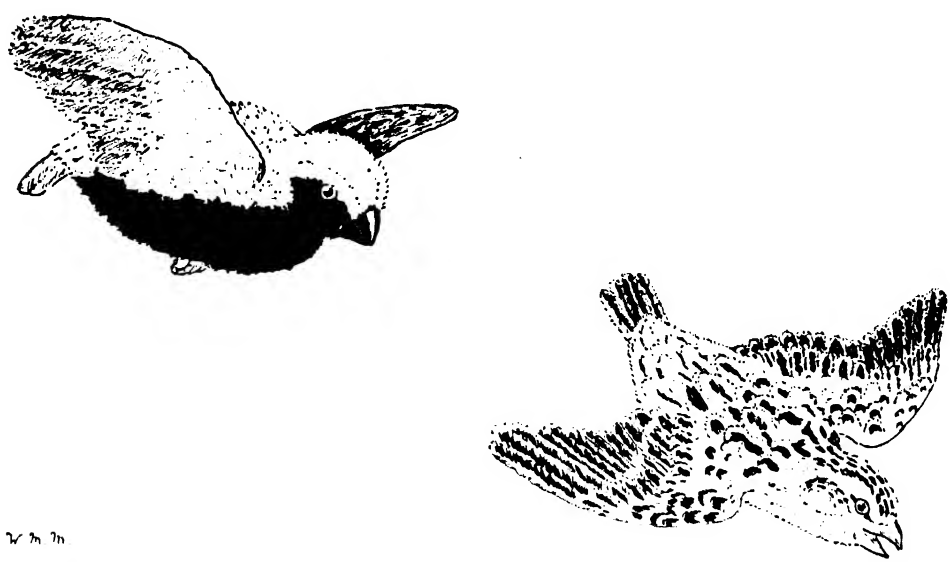


Fig. 1. Male and female *Euplectes nigroventris* in amorous flight. N.B. Male is red and glossy black; female dappled.

2. *EUPLECTES NIGROVENTRIS*

(*a*) *The environment*

The flood plain occupied by these bishops at Mkomasi traverses *Acacia*-desert-grass country and is dependent, not on the local rainfall of less than 20 in. a year, nearly all falling from March to May, but on the water that comes off the South Paré Mountains. As the locality is only about 1500 ft. above the sea and 5° from the Equator the temperatures are high. Mean standard maxima vary from just under 25° C. in the coldest months, June and July, to 34° C. in the hottest, January and February, and 33° C. in March. The corresponding minima are about 16 and 22° C. The eco-climate in the vegetation inhabited by the nesting bishops undoubtedly differs from that of the "standard climate", but the nature and extent of the difference depends on the type of vegetation and the height at which the nests are built (cf. Geiger, 1927; Normand, 1938).

The biological low ebb in the flood plain is from the beginning of August onwards, when the dry season has already lasted some weeks. Except for the perennial water plants, bulrushes and reeds (*Phragmites mauritianus*),[1] the vegetation is all withered and "laid"; none of the *Euplectes* or other weavers are breeding, although they are present in innumerable flocks out of plumage and are still able to find plenty of fallen seed to live on. In some years, but not all, the desiccation is progressive, with increasing heat, until the "long rains" break in March; and annually during this period the weaver birds, including the *Euplectes*, always gradually disappear to some unknown destination.

If the "short rains" of October to December are exceptionally heavy in the mountains, or even in the event of a single cloudburst there, the riverain strip at Mkomasi becomes more or less flooded and in a short time well supplied with the important food grass, *Echinochloa haploclada*. Very few weaver birds of any species breed during that spell of what appear to be suitable conditions; but every year in March, April and May immense numbers of *Euplectes nigroventris*, *Quelea erythrops*, *Q. aethiopica*, *Ploceus aureoflavus*, *P. bojeri*, *Coliuspasser eques* and *Urobrachya axillaris*, with a few weavers of other species, nest in the rich vegetation of the sodden ground. Whenever the flood plain is wet enough a large proportion of it is put under rice.

The *Coliuspasser* and *Urobrachya* occupy very extensive territories, often superimposed on those of *Euplectes nigroventris* with the minimum of mutual interference. The Queleas breed in seething masses that break down even the bulrushes, and though the bishops do not altogether avoid their neighbourhood it would be impossible for effective territory to be extended over one of these "ecological slums". The *Ploceus* spp. breed in specific colonies of a score or two of nests, the site of which may be wholly within bishop territories. Since these golden weavers are active, noisy, blundering and much more robust than the bishops, one would have expected the latter to avoid their proximity. A cock bishop can chase away a female *Ploceus* that comes too near one of his nests, but although he may threaten a cock *Ploceus* we have seen the latter drive him nearly down into the water under the nests. Although they seem such riotous neighbours, we have no evidence that the golden weavers do any actual damage to the bishops' nests. They steal material from each other but probably the bishops' grasses are too slender to attract them.

(*b*) *The physical nature of the territories*

The breeding habits of *Euplectes nigroventris* resemble those of *E. hordeacea* described by Lack (1935). The males are polygamous, they "sing", display and patrol their boundaries similarly. They are even more disinclined to perch in trees of any height and they spend their lives within about 15 ft. of the ground. As in *E. hordeacea*, the males build the skeleton of the nest, and their part is

[1] We are indebted to Mr P. J. Greenway for the botanical names used in this paper.

completed very rapidly. At 13.00 hours on one day a male was tying his first cross-strands between two upright *Phragmites* stems; by 17.00 the next day his "net-purse" had taken its final shape. In this stage, when it can be seen through at all angles, it is occupied by a female, who, while laying (usual clutch 3, maximum 4), thickens the sides and the bottom with the flowering heads of grasses. During this stage the males are attentive, greeting their mates when they arrive, often sitting close to them while they work, visiting the nest in their absence, and bringing material—but not adding it to the structure. Thereafter the male's interest wanes; the incubation and care of the young are solely the task of the female, who brings insects as well as seed to the nestlings. The male builds other skeleton nests in his territory and they are occupied in rapid succession.

In the Mkomasi flood plain we have observed territories of the following types and occasionally territories not confined to a single type:

(1) In pure stands of *Phragmites*, territories from 9 sq. yd. (fully functional) up to about 120, containing no seed and the minimum of insects. Some of these territories abut on patches of the food grass *Echinochloa*, others do not; some overlap *Ploceus* colonies, others do not.

(2) In pure stands of bulrushes, which also provide no food, territories varying from 60 to over 1000 sq. yd. Some are very heavily infested with *Quelea* and *Ploceus* colonies; only a few abut on *Echinochloa*; most are surrounded by *Phragmites*, bulrushes or the grass *Sporobolus robustus*, which is not eaten by the bishops. Birds so situated have to fly some distance, crossing other *Euplectes* territories, to get any food.

(3) In a consocies of *Echinochloa* and the shrubby herb *Hygrophila spinosa*. No such territories are smaller than about 200 sq. yd. They contain a great deal of food and are not infested with the colonial weavers, though *Coliuspasser* and *Urobrachya* nest in this consocies. A disadvantage of this vegetation is that it is often destroyed for cultivation.

(4) In a mixture of herbage, largely the grass *Sorghum verticilliflorum*, with *Solanum* sp. or *Cyperus* sp., or some *Echinochloa* and *Hygrophila*. Territory size as in type (3), containing proportionately less food but still ample. Other nesting weavers are not common, but the predatory lark-headed cuckoo, *Centropus superciliosus*, may be present. This type escapes disturbance for cultivation because it is developed too late in the season.

It appears that bishops established in types (3) and (4) habitually feed within their own territories; therefore while nesting they can take no part in the rice-eating that is sometimes charged against this species. The bishops of types (1) and (2), which have to fly out of their territories for all their food, seem to make indiscriminately for *Echinochloa* not in a bishop territory or for rice unguarded by its human owners, but further observations on this point are required.

Territories of types (1), (2) and (3) rarely provide any particular vantage point for the owner, or contain an obviously favourite perch as is usual in a territory of *Euplectes hordeacea*. Clearly, then, these adjuncts are not necessary for *E. nigroventris*, but none the less they are utilized if available. For example, a few *Sorghum* heads that overtopped a predominantly *Echinochloa* territory

were constantly used by the owner; and a male with a small territory in bulrushes spent much time on a palm stump just clear of their edge.

Some of the boundaries, especially in the smallest territories, are most rigidly kept. Birds may be seen climbing up and down reed stems within a foot of one another, making hostile gestures and noises, but never attacking. Continued observation shows that the mutual boundary has been fixed between those two stems which are so close together. Nevertheless invading males are able to carve territories out of others that are already small and already contain nests.

It will be seen that the variety of vegetation occupied for nesting is great; some territories have not a botanical feature in common except the general habit of the growth. There is also very wide variation in the amount of overlapping with, and disturbance from, breeding birds of other species. In size the territories vary from 9 to at least 1000 sq. yd.; there is no connexion between their size and the availability of food either within their boundaries or in proximity; both the largest and the smallest territories we have seen contained no food plant whatever. On the other hand, the territories that are well supplied with food are as a rule of moderate size, often about 250 sq. yd.

At the height of the nesting season there is always suitable ground unoccupied. But territories containing no food and suffering the maximum of disturbance from other species can be found crowded together more closely than territories in areas possessing neither of these disadvantages. For example, bishops had several co-terminous territories averaging 60 sq. yd. in bulrushes infested with *Ploceus*, while 50 yd. away a bed of bulrushes began that in 2000 sq. yd. contained no bishop or other weaver. And territories of 9 and 15 sq. yd. existed in *Phragmites* simultaneously with territories of 500 sq. yd. and more in bulrushes and of 300 sq. yd. in *Echinochloa*.

(c) *Specific phenology*

So far as the vegetation is concerned, territories of types (1) and (2) could be established at any time of the year; in type (3) when the water has ceased to stand but the ground is still thoroughly wet; in type (4) not until the ground has dried. Most of the early nests are naturally in types (1) and (2), but we have known a bird stake out a claim in type (4) several weeks before any vegetation in it had grown up sufficiently to hold a nest. Thus, as the breeding season progresses, the area eligible for bishop territories increases, by the addition of patches full of the food grass and free of the golden weavers; but we think that the males already established in sites lacking these advantages do not ordinarily transfer themselves.

In 1935 the vegetation was at its best for the *Euplectes nigroventris* by 23 March, territory was being held and nests were occupied. Breeding was still active on 16 June, and on 13 July a few birds, though with diminished territorial instincts, were still in plumage and with occupied nests.

In 1936 conditions were already good by 9 February. A few males were in plumage and had nests, but the great majority were still only coming into breeding condition. On 8 March some males were still not fully red but the majority were breeding hard. We could not visit the place again that year.

In 1937 small patches of suitable vegetation existed during January and February but no bishops were in plumage. On 20 March ample areas of *Echinochloa* were full grown and in seed; some red males were about but we could find no territories. On 24 April activity was at its height; on 20 June not a single *Euplectes nigroventris* in plumage remained, though in spots the vegetation was at least as favourable for continued nesting as it was at the same date in 1935.

About the end of November 1937, exceptional rains produced what seemed optimum breeding conditions. Large numbers of red *E. nigroventris* appeared, took up territory and by 18 December were building. After 29 December no more rain fell, and on a visit on 15 January we found that the whole breeding impulse had been abortive and territories had been abandoned, although the vegetation was still good and red males were common. Reliable native evidence showed that these conditions continued, but very few birds nested for the next three months. At the beginning of May 1938, a sudden recrudescence of activity must have taken place, because on 15 May we found some dozens of nests with eggs but not one with young. By 10 June very few occupied nests and red males remained.

The foregoing observations, discontinuous as they are, show that the dates when the bulk of the *E. nigroventris* come into plumage and breed, vary from year to year in the same locality; but not in such a way as to take advantage of early plant growth. Regardless of the state of the vegetation, breeding ceases at least a month earlier in some years than others, even when it started late. The effective breeding season of the main population varies in different years from under two months to nearly four. We are at a loss for an explanation. Temperature variation from year to year is unlikely to be significant because in these very low latitudes it rarely exceeds 1·5° C. in any given month.

(*d*) *Reproduction rate and sex proportion*

Though we still lack exact fledging and incubation periods it is certain that the young cannot become self-supporting in less than 6 weeks after the first egg of the clutch is laid. Since the nesting season averages barely 3 months, it appears that however frequently each female lays she could not bring up more than two families, together averaging five young, in a year. The maximum number of active nests we have found at the same time in a single territory is five with eggs or young (and two in building), all within a circle of 5 yd. radius in *Echinochloa*. To find four occupied nests at once in a territory is common. One male at the end of the season (13 July) had, in an area of about 10 sq. yd., one nest with three newly hatched young, one with a single fledgling about to

fly, six used nests and one incomplete. The size of the territory could not be ascertained; the male though still present and red, had ceased to keep his boundaries.

It appears then that a successful male commonly attracts four hens at the same time and that up to eight families may be raised in his territory during the season. If all survived, this would give about twenty progeny to each successful male. We do not know of many possible natural enemies, but since we could not get the full history of any individual nests we have no mortality statistics. Destruction of vegetation by man is probably the most potent local check.

An important point, applicable with equal force to *Euplectes hordeacea*, is that although after the breeding season is well under way each territory contains about four females to one male, very few "landless" red males are seen. Thus in any given breeding population the females outnumber the visible males by four to one at the least. This agrees with our observation in early March, just before the mixed flocks broke up, to the effect that the birds showing some signs of the red male plumage numbered about one-seventh of several feeding flocks counted. This result might be brought about in several ways: (1) By genetical sex disproportion. (2) By differential mortality in the nest. (3) By differential mortality after leaving the nest. (4) With an equal average life-span in the two sexes, by the males either attaining sexual powers later in life than the females or losing them earlier.

Possibility (4) can probably be ruled out; for this cause to be effective unaided the sexual life of the average male could only be about one-quarter as long as that of the average female. Also a consequence would be that during each breeding season three-quarters of the male population would be non-functional. Flocks are not to be seen in the breeding areas but non-breeding males might collect elsewhere; or if they did not flock they usually would be accepted by an observer as females. Against late sexual maturity, it may be recalled that Vaughan (1930) collected a red male with frontal bones still incompletely ossified.

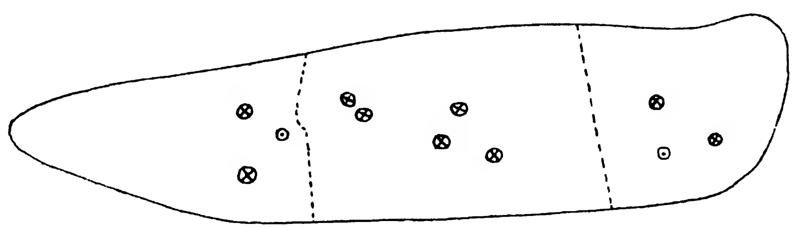
Regarding (3) it can only be said that the conspicuousness of the males does not seem to make them a special butt for predators; we have never seen one taken and we know that with *E. hordeacea* most of the territories repeatedly observed retain their identity, and hence presumably the same owners, throughout the breeding season. As regards possibility (2), in our experience the proportion of broods that number three at a late nestling stage does not appear to be much less than the proportion of clutches with three eggs; but we have no bulk of statistics.

We are left with possibility (1) which, if established, would be of much interest. We accordingly collected about twenty-five nestlings. By the kindness of Mr N. B. Kinnear they were submitted to several zoologists in succession, one of them with special experience in sectioning avian gonads. Our

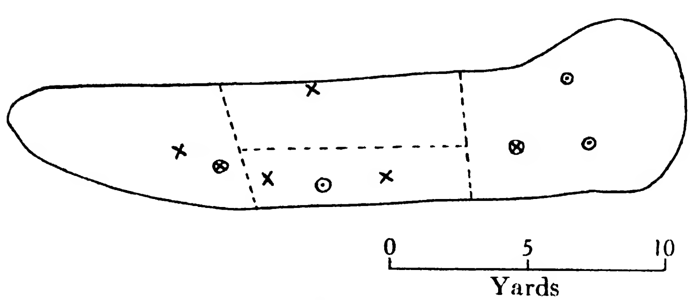
thanks are due to them for the time they spent on our problem; but to our surprise, and theirs, they all failed to find any evidence, microscopic or macroscopic, of the nestlings' sex. There for the time being this interesting problem rests; but we are attacking it by rearing young taken from the nest.

(*e*) *History of a particular site* (*extreme case*)

A strip of pure *Phragmites* with sharply defined edges has retained its identity in 1935, 1936 and 1937, and its surroundings, on one side a railway bank with some low herbage, on the other almost bare alkaline ground, have not changed. Its area has varied between about 50 and 100 sq. yd., with greatest breadth at any point 5 yd.



A. 4 May 1935



B. 9 March 1936

Fig. 2. Occupation of the same patch of reeds by *Euplectes nigroventris*. × Unoccupied nest, ⊗ nest with eggs; ⊙ nest with young.

On 23 March 1935, when breeding was already general, this *Phragmites* strip was about equally divided between two *Euplectes nigroventris* males, one of which had one new nest and the other two, including one with a female (no eggs). On 4 May 1935 (Fig. 2 A), a third male had established himself, and in territories of 30, 35 and 40 sq. yd. respectively there were (*a*) two nests with eggs and one with young; (*b*) five nests with eggs; (*c*) two nests with eggs and one with young. Later in the month the whole strip was destroyed by human agency. The *Phragmites* soon grew up again and on 9 March 1936, that is, quite early in the season, four males had territories which were rigidly defined, in the space of 70 sq. yd. (Fig. 2 B). It is unfortunate that we were not able to observe further developments.

In 1937 the *Phragmites* was less close and well grown than in the two preceding years. On 20 March 1937, it was unoccupied; on 24 April, one *Euplectes nigroventris* was in undisputed possession of the whole strip, with one skeleton nest and one to which a female was adding; on 20 June the birds were gone and no sign remained of how many nests they might have had.

3. *Euplectes hordeacea*

(*a*) *The environment*

The localities between Amani and the coast at which we have observed this species, including the area studied by Lack (1935), to which we have given special attention, are all at altitudes below 1000 ft. with a fairly well distributed rainfall of 45–60 in. (according to locality). The bulk of this comes with the "long rains" of March to May, and most of the remainder with the "short rains" of October to December, but rainless months at any season are exceptional. The standard temperatures are not quite so high as in the *E. nigroventris* area at Mkomasi, but the yearly course is the same with mean maxima about 33° C. in February and March.

A consequence of the well-distributed rainfall is that suspension of plant growth is not so complete as in the *E. nigroventris* station just discussed. In the highest rainfall area, at the foot of the East Usambara Mountains, which includes Lack's area, the pioneer on ground that has been cleared is the rank harsh grass *Rotboellia exaltata*, the staple food of the nesting *Euplectes hordeacea*, and one that forms dense masses, often in pure stands of a quarter of an acre or more, 10 ft. tall. Its associates are the grasses *Panicum maximum*, also rank-growing and bristly *Sorghum verticilliflorum*. The latter is a favourite nesting site but the former is probably not rigid enough. All these grasses make their chief growth of the year on the "long rains" and seed and wither in the subsequent cool and comparatively dry season. Much new growth takes place on the "short rains", and in spots that have not been cleared *Rotboellia* is ousted by its two associates. Further stages in the succession are the appearance of the mat-grass *Panicum tricocladum*, which the bishops cannot eat or nest in, woody herbs, such as *Vernonia* sp., and bushy growth, a stage in the succession to evergreen forest. Since *Euplectes hordeacea* nests only where there is plenty of tall grass and prefers areas with *Rotboellia*, the same piece of ground does not usually remain equally attractive to this species in successive years.

Other birds that occupy ground attractive to *Euplectes hordeacea* are the very similar *E. capensis*, the much more extensive territories of which overlap those of several *hordeacea* without much mutual interference, and the cut-throat whydah, *Coliuspasser ardens*, a smaller and weaker bird than *Euplectes hordeacea*, but one whose presence seems to cause a certain amount of annoyance. Especially where clumps of *Pennisetum purpureum* are present small

groups of *Ploceus aureoflavus* or *Amblyospiza albifrons* may nest; but the territories of *Euplectes hordeacea* are so much bigger than those of *E. nigroventris* that the presence of such colonial species is of comparatively much less importance.

(b) *Specific phenology*

During the off season this bishop is little seen in the areas where it nests and it drifts about the country in dull-plumaged flocks. We have very rarely seen males in the red nuptial dress between mid-October and the end of February inclusive and then only odd ones, apparently not breeding, though they occasionally breed about October in Zanzibar (Vaughan, 1930). Every year a few can be found in full plumage in early March, but it is not until early May, that is in the latter half of the "long rains", that red males are in their maximum abundance. So far as the vegetation and food supply are concerned, we know of no reason why breeding should not take place also in December and January.

In 1934 when Lack (1935)[1] made a detailed study of a nesting area of these bishops, it is not known exactly when the territories he recorded were taken up; but we had found newly hatched young in the district as early as 8 June. Making occasional observations on his territories after he returned to England we found that on 29 September most were still occupied, but one or two of the owners were going out of plumage and were noticeably more tolerant of trespassing males. On 4 October the situation was similar, but by 21 October, when the grass was very dry and brown, not a bishop remained.

In 1935, when we had intended duplicating the observations of 1934, the usual few full-plumaged males were in the district in March, and on 31 March we found a newly begun nest near Tanga. The vegetation in the area including Lack's territories that year was, however, quite different. *Rotboellia* had practically ceased to exist; in territories 2, 4, 5 and 6 the erect *Panicum maximum* was a very strong dominant and in 1, 3 and 7 the mat-grass *P. tricocladum*. Throughout the 1935 season the site of the 1934 territories was unoccupied.

Elsewhere in the vicinity the 1935 season proved to be abnormal. Throughout June, July and August mixed flocks of females and full-plumaged males could be seen moving about and feeding. (In 1934 Lack found mixed congregation only at the drinking-place.) On 4 August we devoted some hours to watching a patch of *Rotboellia* in which three full-plumaged males at first seemed to have established territory; but we soon found that they showed great tolerance of passing males, took no notice of mixed flocks, and on the next day were not in their supposed territories at all.

[1] For purposes of this paper we have been able to refer to a manuscript plan of Lack's, from which he extracted and simplified his published figure.

In fact during the 1935 season we failed to observe any breeding near Lack's area (though we did elsewhere in the Tanga District). On 12 August, four full-plumaged males collected from mixed flocks had testes already deflating; a week later birds in half plumage and with quite small testes were common. Thus in 1935 the phenology was very different from that of the preceding year; the breeding impulse seems to have been locally deficient and breeding plumage disappeared nearly two months earlier.

In 1936 we were away from Africa on leave. In 1937 events followed closely those of 1934 and the vegetation of Lack's main area was similar to what it had been then, with plenty of *Rotboellia, Sorghum verticilliflorum* and *Panicum maximum*, but no mat-grass. The area on the north of the road, to which in his figure three territories were shown extending, had, however, made uninterrupted bush growth, so that ground attractive to bishops no longer existed on that side. We can say that territories were established between 15 May and 13 June, though unfortunately illness prevented us from fixing the date more nearly.

As in 1934, the birds seemed to get all their food in their territories and did not visit patches of rice and maize a few hundred yards away. Most of the territories we recorded in June were still intact, with very little alteration of their boundaries, in the middle of August, when no males showed any signs of going out of plumage and nests containing eggs were still common. Thereafter the territories dissolved rapidly. In one group of originally ten only three still held active males on 6 September, and these were abandoned by about 21 September. Three days later a few males were still in the area but they were going out of plumage and had lost their possessiveness. Thus in 1937 the males' activity lasted for between three and four months. It was over nearly a month earlier than in 1934.

On 6 October not a single male was visible; but in a spot that we believe to have been contained in the territory of one of those still present but going out of plumage on 24 September, three females were traced to nests in which they were feeding very small young. The first of the eggs from which these came must almost certainly have been laid about 20 days before, i.e. about 16 September. The inference is that the procreative and the territorial instincts of the male remain active about equally long and fade together—in this instance at the same time as the red plumage begins to go. Also, the females were occupied with a part of their breeding cycle for an appreciable period after the males' had come to an end.

(c) *The territories on the same ground in* 1934 *and* 1937

We found that the main conclusions reached by Lack (1935) in 1934 held good in 1937, namely, that the size and the boundaries of the individual *hordeacea* territories have no relation to the amount of the food plant available in each, nor to topographical features. Personally we have so far not seen a

territory that did not consist largely of tall grass; but the composition of the grass occupied varies from practically pure *Rotboellia* to *Panicum maximum* with a little *Sorghum verticilliflorum* or *Cleistachne sorghoides*.

An important general point of difference in the 1937 season was that the boundaries at no time became so rigidly defined as in 1934, when persistent patrollings fixed them within 2 or 3 ft. As a result of the lack of pressure from contiguous owners the boundaries were not as a rule so straight and the territories tended to be irregularly oval rather than rectangular. Correlated with this was the fact that there was more unoccupied interstitial ground, some of which looked to be most eligible.

In the area of about 16,000 sq. yd. taken by Lack the greatest number of territories that could be traced was nine complete ones and part of two others. This gives an average of 1600 sq. yd., compared with 925 in 1934; but owing to the interstices the average area effectively controlled did not exceed 1100 sq. yd. The minimum was about 600 and the maximum not more than 1500.

The combined area of territories II to VI in Lack's plan (1935) held in 1937 only two territories and part of a third. A strip from 10–15 yd. wide bordering the road was not occupied by any birds either in this particular patch or elsewhere in either direction. We can adduce no external reason for this. It seems most likely that occupation in that year was forced nearer the road by the heavier bishop population.

With two exceptions, the ten territories of June 1937 were maintained with hardly any alteration until mid-August, although, as explained, most of the boundaries were not fixed by constant pressure from both sides. The exceptions were contiguous. One of them apparently lost its owner early in July. At the beginning of August the favourite perch of the male in the other territory was taken over by a yellow bishop. At the same time a male *hordeacea* appeared in interstitial ground alongside and began to act territorially, but a few days later was gone.

Other observations we made in 1937 in the same piece of country led us to similar general conclusions; in suitable grassland we found a mosaic of persistent territories usually not much exceeding 1000 sq. yd. but with large interstices. On the other hand in another part of the Tanga District on 2 June 1935 a block of pure *Rotboellia* 80 by 45 yd. (sharply marked off by surrounding native cultivation) was completely divided between six males. Their average territory was thus 600 sq. yd., but one was particularly small, not exceeding 200 sq. yd. Nesting was only just beginning, so it was impossible to say how far the little territory was functional.

To sum up: of about fifty territories worked out, and for the most part repeatedly observed, by Lack and by us, only five covered less than 600 or more than about 1200 sq. yd. In 1937, when the local population pressure was not so great as in 1934, the territories were bigger, but only by about 20 %, when occupation of all the suitable interstices would have increased them by 75 %.

It is a reasonable inference that at least in the Tanga District *Euplectes hordeacea* has a specific territory size of 900 ± 300 sq. yd. irrespective of the specific composition of the grass, provided that it is of the right habit.

4. Comparative Summary

Both *E. nigroventris* and *E. hordeacea* have breeding seasons that are shorter than the vegetation growth would allow. The specific climatic relations are rather different: *E. nigroventris* already has young when the daily maximum temperatures are still nearly at their highest and it continues to breed, through the long "long rains" and on a falling temperature, till the middle of the cool season; *E. hordeacea* breeds at the end of the "long rains" in the coolest months of the year. These specific temperature relations may not be of significance. In Pemba, where the climate is very like that of the East Usambara foothills, Pakenham (1936) found eggs and young of *E. hordeacea* in the hottest months as well as the coolest. Both species vary in the date that breeding condition becomes general and to a striking extent in its effective duration in the same locality in successive years. No reason for the variation can be suggested.

In neither species does the size or the position of the territory bear any relation to the availability of food for adults or young, or to topographical features. *E. hordeacea* territories, however, always in our experience consist largely of grass, while those of *E. nigroventris* may contain none. The great majority of *E. hordeacea* territories occupy 900 ± 300 sq. yd., an area not much affected by abundance of breeding males. Thus in *E. hordeacea* size of territory is possibly specific. *E. nigroventris* on the other hand is almost indefinitely compressible, and moreover its smallest territories are often those with the most obvious disadvantages of lack of food and of crowding by other species. It is probable, in fact, that fully functional *E. nigroventris* territories of under 10 sq. yd. are the extreme examples among those of Passerine birds in which territorial behaviour is developed typically.

Irrespective of the size of his territory a male *E. nigroventris* has up to five breeding females active in it at once and may raise eight families in it during the season. In a territory of *E. hordeacea* not more than three breeding females have been found at once. In the breeding population of both species females outnumber males by quite four to one. We are trying to ascertain whether this difference is genetical.

The foregoing conclusions regarding the territories of the two species are highly relevant to the discussion summarized by Lack (1937). In particular they show that in one species the specific territory size can, on present evidence, be regarded as a limiting factor in population density, while in another, closely allied and with generally similar habits, this possibility is excluded. In the "compressible" species the suggestion of any food motive in the territorial habit can be ruled out with exceptional conclusiveness. Finally, the smallest

territories of the "compressible" species are not obviously less successful than any others of either species.

REFERENCES

Geiger, A. (1927). "Das Klima der bodennahen Luftschicht." Braunschweig.

Lack, D. (1935). "Territory and polygamy in a bishop-bird, *Euplectes hordeacea hordeacea* (Linn.)." Ibis, 5: 817–36.

Lack, D. (1937). "A review of bird census work and bird population problems." Ibis, 1: 369–95.

Moreau, R. E. (1935). "A synecological study of Usambara, Tanganyika Territory, with particular reference to birds." J. Ecol. 23: 1–43.

Normand, C. W. B. (1938). "Report of the Agricultural Meteorology Section, Indian Meteorological Department, for the period 22nd August 1935 to 31st March 1937." New Delhi.

Pakenham, R. H. W. (1936). "Field-notes on the birds of Zanzibar and Pemba." Ibis, 6: 249–72.

Reichenow, A. (1904–5). "Die Vögel Afrikas." Vol. 3. Neudamm.

Vaughan, J. H. (1929, 1930). "The birds of Zanzibar and Pemba." Ibis, 5: 577–608, and 6: 1–48.

AN ECTOPARASITE CENSUS OF SOME COMMON JAVANESE RATS

By GORDON B. THOMPSON

(*With Plate* 14)

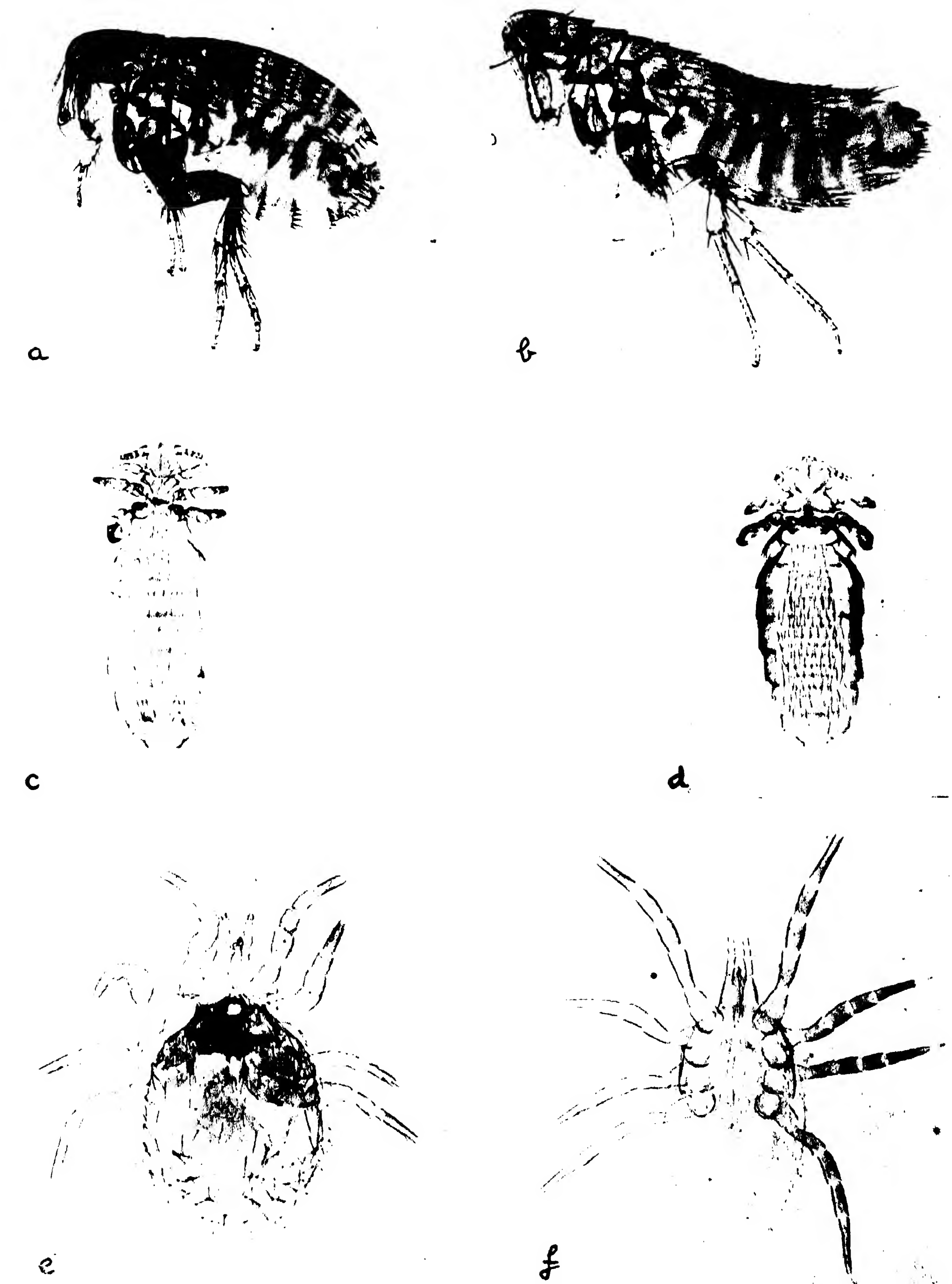
EXCEPT for my recent paper (Thompson, 1938*a*) containing a census of ectoparasites of the common Ceylon rat (*Rattus rattus kandiyanus* Kelaart) I do not think anything in the nature of a complete census of rat parasites has been published. This paper contains a complete analysis of the ectoparasites collected from 73 specimens of *Rattus rattus diardi* (Jentink) by Dr Felix Kopstein, to whom I am indebted for the opportunity of studying this unique collection. He is to be congratulated on the excellent manner in which he has collected all this material.

Rattus r. diardi is the common Javanese rat and much has been written about it, mostly by Dutch naturalists. It was first recognized as a distinct form by Jentink in 1879, but since that time has been relegated to the status of a subspecies of *Rattus rattus* (i.e. the black rat). Originally described from West Java, it seems to occur commonly throughout the island. According to Tate (1936) "the consensus of opinion is that the species is somewhat variable and about seaports may hybridize with exotics such as *alexandrinus* and *rattus*". In view of these facts it plays an important part in the question of distribution of rat fleas. Dr Kopstein has published three papers (1931, 1932 *a*, *b*) dealing with this aspect of Javanese fleas in relation to plague.

I do not propose to deal with the question of rat fleas and their relation to plague epidemics in this paper but merely to present a detailed table of all the ectoparasites found on specimens of this common rat and to draw attention to certain significant facts presented by the figures. Of the four groups of ectoparasites (ticks, mites, fleas and lice) which one might expect to find on rats, all are represented in the collection under discussion save ticks. I think it can be safely said that we have here a very good representation of the various groups of ectoparasites, except for small mites such as species of *Myobia* which are very minute and difficult to collect on a large scale. All these parasites are blood suckers.

In the accompanying table all the ectoparasites have been counted carefully, and all save the Acarina or mites have been sexed. The mites were far too numerous to permit a count of sexes; the numbers of mites must therefore be taken to include both adults and immatures. In dealing with the fleas I have received a great deal of help from Dr Julius Wagner—the well-known authority on the Siphonaptera. The remainder of the groups have been dealt with for the most part by me.

Of the 73 rats examined, 18 bore lice (i.e. 25 %), 26 bore fleas (i.e. 36 %) and 41 bore mites (i.e. 56 %). (The percentages are only approximate.)



(*a*) *Xenopsylla cheopis*; (*b*) *Stivalius cognatus*; (*c*) *Polyplax spinulosa*;
(*d*) *Hoplopleura oenomydis*; (*e*) *Laelaps echidninus*; (*f*) *Liponyssus* sp.

Those specimens of rats carrying fleas seem to be completely devoid of any other kind of parasite whereas rats carrying lice usually have mites but no fleas. Of the 26 rats carrying fleas 20 were collected at altitudes ranging from 600 to 2100 m., one at 482 m. and five in coastal districts. Rats collected above 1000 m. seem to be more heavily infested than those at lower altitudes. The females of the parasites are very much in excess of the males.

Four species of fleas occur on this rat. The two species of *Xenopsylla* are well known from their association with plague epidemics, *Xenopsylla cheopis* is the commoner species but both the species seem to have a very wide tropical and subtropical distribution with rats as their hosts. Only two specimens of the common cat flea *Ctenocephalides felis* were found. Rats are not the normal hosts of this flea, but owing to rats' association with man's habitations they frequently carry them. The fourth species, *Stivalius cognatus*, is a much larger flea than the others, and belongs to a group, which is very abundant in the Indo-Australian region. It is the commonest species of *Stivalius* occurring in Java and appears to be confined to that island, where it has been recorded as parasitizing at least eight species of the genus *Rattus*, together with a few other closely related hosts.

With regard to the lice, two species, *Polyplax spinulosa* and *Hoplopleura oenomydis*, occur on *Rattus r. diardi*. In a recent paper (Thompson, 1938*b*) I have pointed out the significance of the occurrence of these two species of rat lice and the light which they throw on the distribution of the rats. I do not propose therefore to say any more here regarding them except to urge the need for careful collection of rat lice from the Indo-Australian and Pacific regions. Mites are the most abundant parasites of these rats in Java. *Laelaps echidninus* is the commonest species and is known to occur on rats in various parts of the world. It is particularly abundant in the tropics. Although the numbers given in the table for this species represent the gross number of individuals, an estimate of the sexes was made of a few samples. The percentage of males was found to be very low (i.e. approx. 4 %).

Referring again to the question of the different groups of parasites occurring on individual rats the following table may serve to emphasize the points mentioned previously.

	Fleas	Lice	Mites
No. of rats	24	0	0
	1	0	1
	1	1	0
	0	0	0
	0	12	12
	0	5	0
	0	0	28
	26	18	41

The interesting points are (1) of the 26 rats carrying fleas only two had other parasites, namely one with eight mites and another with one louse; (2) of the 18 rats carrying lice all except six bore mites as well; (3) 28

Table 1.

Ref. no.	Locality, etc.	Siphonaptera: *Xenopsylla cheopis* (Roths.) ♀	♂	*Xenopsylla astia* Roths. ♀	♂	*Stivalius cognatus* J. & R. ♀	♂	Siphunculata: *Hoplopleura oenomydis* Ferris ♀	♂	*Polyplax spinulosa* (Burm.) ♀	♂	Acarina: *Laelaps echidninus* Berlese No. of specs.	Undetermined species No. of specs.
1	North Coast, Tegal, Dec. 1934	.	.	.	.	.	.	3	.	1	.	.	.
14	,, ,, ,, Nov. 1934	.	.	.	.	.	.	.	.	.	.	×	.
15	,, ,, ,, Nov. 1934	.	.	.	.	.	.	.	.	.	.	×	.
61	,, ,, ,, 26 June 1930	.	.	.	.	.	.	3	.	.	.	77	3
40	,, ,, Cheribon, Dec. 1930	.	.	.	.	.	.	1	.	.	.	57	.
43	,, ,, ,, Weroe, 6 Aug. 1931	.	.	.	.	.	.	.	.	18	5	.	.
68	,, ,, ,, ,, 6 Aug. 1931	.	.	.	.	.	.	.	.	.	.	4	8
72	,, ,, nr. Cheribon, Soeranengala, 9 May 1930	.	.	.	.	.	.	.	.	1	.	111	3
67	,, ,, Semarang, Oct. 1930	.	.	.	.	.	.	.	.	.	.	8	9
74	,, ,, nr. Indramajoe, Pabean Ilir, 27 Jan. 1932	1	1	.	.	.	.	.	.	.	.	.	.
25	East Coast, Banjoewangi, 25 July 1930	3	1	5	3	.	.	.	.	.	.	.	.
55	,, ,, ,, 23 July 1930	.	.	.	.	.	.	.	.	.	.	6	.
77	,, ,, ,, 22 July 1930	2	2	1	2	.	.	.	.	.	.	.	.
82	East Java, Tosari, 1800 m., 20 Sept. 1930	.	.	.	.	.	.	.	.	.	.	.	.
84	East Coast, Soerabaja, Sept. 1931	15	10	.	.	.	.	.	.	.	.	.	.
107	,, ,, ,, Sept. 1931	18	16*	.	.	.	.	.	.	.	.	.	.
3	Mid-Java, Temanggoeng, 583 m., May 1933	.	.	.	.	.	.	.	.	4	.	.	.
4	,, ,, 583 m., May 1933	.	.	.	.	.	.	.	.	.	.	9	4
6	,, ,, 583 m., May 1933	.	.	.	.	.	.	.	1	5	1	58	10
12	,, ,, Kabloekan, 630 m., April 1933	.	.	.	.	.	.	.	.	.	.	×	.
13	,, ,, ,, 630 m., April 1933	.	.	.	.	.	.	.	.	.	.	×	.
10	,, Kranggan, 482 m., Oct. 1933	3	3	.	.	.	.	.	.	.	.	.	.
11	,, ,, 482 m., Oct. 1933	.	.	.	.	.	.	.	.	.	.	×	.
83	,, Diëng Koelon, 2100 m., 8 July 1931	1	.	.	.	2	4	.	.	.	.	.	.
106	,, nr. Wonosobo, Kedjadjar, 1427 m., 11 July 1931	.	.	.	.	5	5	.	.	.	.	.	.
20	West Java, Lembang, 1250 m., May 1931	3	1	.	.	.	.	.	.	.	.	.	.
31	,, ,, ,, 1250 m., May 1932	.	.	.	.	.	.	.	.	.	.	34	.
36	,, ,, ,, 1250 m., May 1931	.	.	.	.	.	.	.	.	.	.	48	.
51	,, ,, ,, 1250 m., Oct. 1932	.	.	.	.	.	.	.	.	.	.	27	.
69	,, ,, ,, 1250 m., Oct. 1932	.	.	.	.	3	4	.	.	.	.	.	.

28	West Java, nr. Lembang, Tjiboeriah, 1200 m., June 1932	.	.	.	.	.	.	.	.	.	.	124	.
76	,, ,, ,, Tjikole, 1200 m., June 1932	60	55	.	.	1	2	.	.	.	.	.	.
87	,, ,, ,, Tjiboeriah, 1200 m., June 1932	.	.	.	.	9	14	.	.	.	.	.	.
88	,, ,, ,, Tjikidang, 1300 m., May 1932	196	125	.	.	7	3	.	.	1	.	.	.
22	,, ,, Bandoeng, 750 m., June 1932	.	.	.	.	.	.	1	.	6	.	..	.
30	,, ,, ,, 700 m., June 1932	.	.	.	.	.	.	.	.	.	.	4	.
32	,, ,, ,, 700 m., July 1932	.	.	.	.	.	.	5	.	12	1	580	.
34	,, ,, ,, 700 m., June 1932	.	.	.	.	.	.	1	.	1	.	60	12
45	,, ,, ,, 700 m., June 1932	.	.	.	.	.	.	24	9	58	9	62	4
53	,, ,, ,, 700 m., Aug. 1932	.	.	.	.	.	.	45	3	7	1	390	.
57	,, ,, ,, 700 m., Sept. 1932	.	.	.	.	.	.	110	10	42	6	200	.
102	,, ,, Bandoeng, 700 m., Mar. 1930	.	.	.	.	.	.	.	.	.	.	.	.
46	,, ,, nr. Bandoeng, Tandjoeng Sari, 854 m., July 1932	.	.	.	.	.	.	.	.	.	.	36	.
49	,, ,, ,, ,, 700 m., July 1932	.	.	.	.	.	.	.	.	.	.	50	.
58	,, ,, ,, Artjamanik, 1070 m., 1 June 1930	.	.	.	.	.	.	.	.	.	.	3	.
99	,, ,, ,, ,, 1070 m., 1 June 1930	12	14	.	.	2	4	.	.	.	.	.	.
7	,, ,, Tjiwidej, 1100 m., Feb. 1933	.	.	.	.	.	.	.	.	.	.	9	.
8	,, ,, ,, 1100 m., Feb. 1933	.	.	.	.	.	.	.	.	.	.	12	.
9	,, ,, ,, 1100 m., Feb. 1933	.	.	.	.	.	.	.	.	.	.	30	.
81	,, ,, Soekaboemi, 600 m., Nov. 1931	3	.	.	.	.	2	.	.	.	.	.	.
21	,, ,, Sindanglaja, Tjipanas, 1100 m., Dec. 1931	35	21	.	.	.	.	.	.	.	.	.	.
27	,, ,, ,, ,, 1100 m., 10 Feb. 1931	.	.	.	.	.	.	.	.	8	.	.	.
80	,, ,, ,, ,, 1100 m., 11 Feb. 1931	9	3	.	.	4	1	.	.	.	.	.	.
86	,, ,, ,, ,, 1100 m., Dec. 1931	.	.	.	.	1	1	.	.	.	.	.	.
93	,, ,, ,, ,, 1100 m., Dec. 1931	1	1	.	.	.	.	.	.	.	.	.	.
94	,, ,, ,, ,, 1100 m., 11 Feb. 1931	.	.	.	.	.	.	.	.	.	.	15	.
26	,, ,, Soreang, 740 m., Mar. 1932	.	.	.	.	.	.	.	.	.	.	43	.
90	,, ,, ,, 740 m., 27 Feb. 1932	1	.	.	.	.	.	.	.	.	.	.	.
38	,, ,, Padalarang, 700 m., Sept. 1932	.	.	.	.	.	.	.	.	.	.	44	.
54	,, ,, ,, 700 m., Sept. 1932	.	.	.	.	.	.	1	.	.	.	9	.
63	,, ,, ,, 700 m., 24 Sept. 1932	.†	.	.	.	.	.	.	.	.	.	.	.
64	,, ,, ,, 700 m., Sept. 1932	.	.	.	.	.	.	3	.	.	.	19	2
70	,, ,, ,, 700 m., Sept. 1932	2	2	.	.	.	.	.	.	.	.	.	.
91	,, ,, ,, 700 m., Sept. 1932	1	.	.	.	.	.	.	.	.	.	.	.
29	,, ,, Mt. Gedeh, Tjibordas, Rarahan, 1350 m., 14 Feb. 1932	.	.	.	.	.	.	.	.	.	.	9	1
85	,, ,, ,, ,, ,, 1350 m., 6 June 1933	10	2	.	.	1	.	.	.	.	.	.	.
95	,, ,, ,, ,, ,, 1350 m., June 1930	1	.	.	.	.	3	.	.	.	.	.	.
98	,, ,, ,, ,, Goenoeng, 1300 m., 8 June 1930	3	2	.	.	13	7	.	.	.	.	8	.
105	,, ,, Koeningan, 550 m., 26 April 1931	.	.	.	.	.	.	.	.	.	.	13	.
56	,, ,, coast, Indramajoe, Pabean Ilir, 27 Jan. 1931	.	.	.	.	.	.	.	.	.	.	3	.
71	,, ,, ,, ,, ,, 11 May 1932	.	.	.	.	.	.	3	.	2	.	26	.
60	,, ,, coast, nr. Cheribon, Soeranengala, 9 May 1930	.	.	.	.	.	.	.	.	.	.	29	1
73	,, ,, Buitenzorg, 250 m., 21 Aug. 1930	.	.	.	.	.	.	.	.	.	.	15	.

× I am unable to say how many mites were obtained from these rats. It is possible that other species were present besides *L. echidninus* Berlese.

* 1♀, *Ctenocephalides felis* (Bouché). † 1♂, *Ctenocephalides felis* (Bouché).

rats out of the total of 73 carried mites only. From these facts it may be said that the presence of fleas on a rat indicates an almost complete absence of any other kind of parasite, whereas lice and mites seem to occur together although mites may be present without lice. We know so little of the ecology of these different groups of parasites, taking the host as the ecological unit, that it is almost impossible to draw any conclusions from the facts presented in the present case, but there does seem to be some relationship between the various groups. The large table containing the analysis of the parasites is arranged as far as possible in geographical sequence. This arrangement tends to show a relationship between the habitat and the parasites present on the host. This possibility must not be overlooked when considering the presence or absence of one or more of the parasite groups. It is not yet possible to say whether the presence or absence of one or more of the parasite groups is determined by a habitat factor or by some biotic one on the host. It may be noted here that the fleas spend only their adult life in association with the host, whereas the lice and mites pass their whole existence on the body of the host. The question of antagonism among the parasite groups must also be considered. Little is known regarding this, but in my own experience in the case of birds I have frequently found that the presence of mites in extensive numbers usually indicates an absence of lice. This point is not, however, borne out by the figures in the present case.

For the photographs I am greatly indebted to Dr J. W. Shackle.

Summary

1. A complete census is given of the ectoparasites collected from 73 specimens of the common Javanese rat (*Rattus r. diardi* (Jentink)).

2. 36 % of the rats carried fleas; 25 % carried lice; 56 % carried mites.

3. Rats carrying fleas seldom had any other parasites on them. As a rule, rats carrying lice had mites on them whereas mites were present without either fleas or lice.

4. The presence or absence of one or more of the parasite groups may be determined either by a habitat factor or by some biotic one on the host.

5. Females of the parasite species are far in excess of the number of males.

References

Kopstein, F. (1931). "Die Ökologie der javanischen Ratten und ihre Bedeutung für die Epidemiologie der Pest." Z. Morph. Ökol. Tiere, 22: 774–807.

Kopstein, F. (1932 a). "Die geographische Verbreitung von *Xenopsylla astia* in Java und ihre Bedeutung für die Epidemiologie der Beulenpest." Z. Hyg. InfektKr. 114: 289–301.

Kopstein, F. (1932 b). "Die Ökologie der javanischen Siphonapteren und ihre Bedeutung für die Epidemiologie der Pest." Z. Morph. Ökol. Tiere, 24: 408–34.

Tate, G. H. H. (1936). "Some Muridae of the Indo-Australian Region." Bull. Amer. Mus. 72: 501–728.

Thompson, G. B. (1938 a). "A census of the ectoparasites of some Ceylon rats." J. Anim. Ecol. 7: 71–3.

Thompson, G. B. (1938 b). "Notes on the two species of Siphunculata occurring on *Rattus* spp. in the Malayan and Pacific regions, with special reference to Java." (In the Press.)

SOME OBSERVATIONS ON THE BIOLOGY OF THE TROUT (*SALMO TRUTTA*) IN WINDERMERE

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(*With* 2 *Figures in the Text*)

1. Introduction and methods

The observations upon which this paper is based were obtained while working at the laboratory of the Freshwater Biological Association on Windermere between November 1933 and October 1935.

Windermere is 17 km. in length, and has a mean breadth of 0·9 km. It is a fairly deep lake, with a mean depth of 24 m., and the littoral region is narrow. Across the centre of the lake is a belt of shallow water with numerous islands, and this divides the lake into two basins. The fish examined in the course of this work were nearly all collected in the north or upper basin. It is a lake in an intermediate stage of evolution, and has the fish fauna typical of such lakes. In addition to trout and char (*Salvelinus willughbii*) which are characteristic of primitive lakes, it contains several species usually found in evolved lakes such as pike (*Esox lucius*), perch (*Perca fluviatilis*) and minnow (*Phoxinus phoxinus*). A more complete list of the fish occurring in the lake has been given in a previous paper (Allen, 1935).

The water of Windermere is soft, and has a pH of about 6·8. Pearsall (1930) has published the results of a number of analyses of the dissolved substances in the water of the lake.

Nearly all the fish examined in the course of the work with which this paper deals were collected with a seine net. This net was 46 m. in length and 3·3 m. in depth. It was so mounted that it hung vertically in the water with the upper edge at the surface. In use this net was laid in a straight line parallel to the shore and about 90 m. from it, and was drawn on shore by means of ropes attached to the ends. Thus only fish which were in the surface 3 m. and particularly those close to the shore were caught. A few fish caught by angling are also included in this paper, but these were also caught near the surface and near the shore.

It is, however, known that trout live in the deep water of the lake away from the shore as well as along the littoral region; and it is probable that there are considerable seasonal variations in the proportions of the trout population which inhabit the two environments. Since the paper deals only with trout

inhabiting the littoral region, certain reservations have to be made in applying the results to the trout population as a whole. This matter will be discussed further in a later part of the paper.

2. Growth and seasonal changes

In order to investigate the growth of the trout in Windermere the scales of all trout caught were examined. From this examination the age of the fish, its size at the end of each year of its life, and the age at which it entered the lake were determined. The technique of age determination from scales is now so well known as not to require description. As regards the calculation from scale measurements of the size of a fish at earlier stages in its life, it is the usual practice to assume that throughout life the ratio between length of scale and length of fish remains constant. In the Salmonidae there is as yet no decisive evidence on this point, although Segerstråle (1933) has shown that, for several other species of fish, the ratio may change as the fish grows.

Table 1. *The length in cm. of trout at the end of each winter, the results obtained from fish of different ages being given separately*

Age of fish in years	1	2	3	4	5	6	7	All fish
No. of fish	16	161	174	54	9	3	3	420
Length after 1 year	8·0	6·1	5·4	5·6	5·9	4·1	5·8	5·8
Length after 2 years	—	15·4	12·4	13·0	12·5	11·0	12·3	13·7
Length after 3 years	—	—	21·7	21·8	20·1	17·7	23·1	21·5
Length after 4 years	—	—	—	28·3	29·6	24·6	31·9	28·5
Length after 5 years	—	—	—	—	35·8	31·5	39·9	35·8
Length after 6 years	—	—	—	—	—	36·9	44·7	40·8
Length after 7 years	—	—	—	—	—	—	48·3	48·3
% of total collection	4	38	41	13	2	1	1	—

Table 1, which has been calculated on the assumption that the ratio remains constant, shows the mean calculated lengths of the trout examined at the end of each year of growth. The results for the trout of different ages are given separately. While the calculated lengths based on fish in their third and subsequent years are in good agreement, the figures obtained from one- and two-year-old fish are considerably higher. A change in the ratio between scale length and fish length during the first two years could produce this effect, but since there are two other causes known to exist which could cause the high figures obtained for fish in their first two years it is at present better to assume that the ratio remains constant. One of these causes is the selective action of the net used. This had a mesh of 2·5 cm. knot to knot, and consequently tended to allow fish under 20 cm. in length to escape. Since most fish do not reach this size until late in their third year, the net would tend to select the larger individuals of the one-year and two-year classes (i.e. fish in their second and third years). Thus the calculated lengths based on fish in these classes will be somewhat too high. The other cause of the high figures given by fish in the first two classes depends on the age and size of the fish at migration and will be referred to again later.

In Fig. 1 the mean calculated lengths for all fish are plotted against age and it will be seen that after an acceleration during the first year the growth curve is almost linear. The curve has been extended backward to meet the length axis at 2 cm., since this is about the size of newly hatched fry. This continued steady growth appears to be typical of neutral or alkaline waters, while in more acid conditions the rate of growth usually falls off sharply after two or three years. As a contrast with the conditions found in Windermere, the following

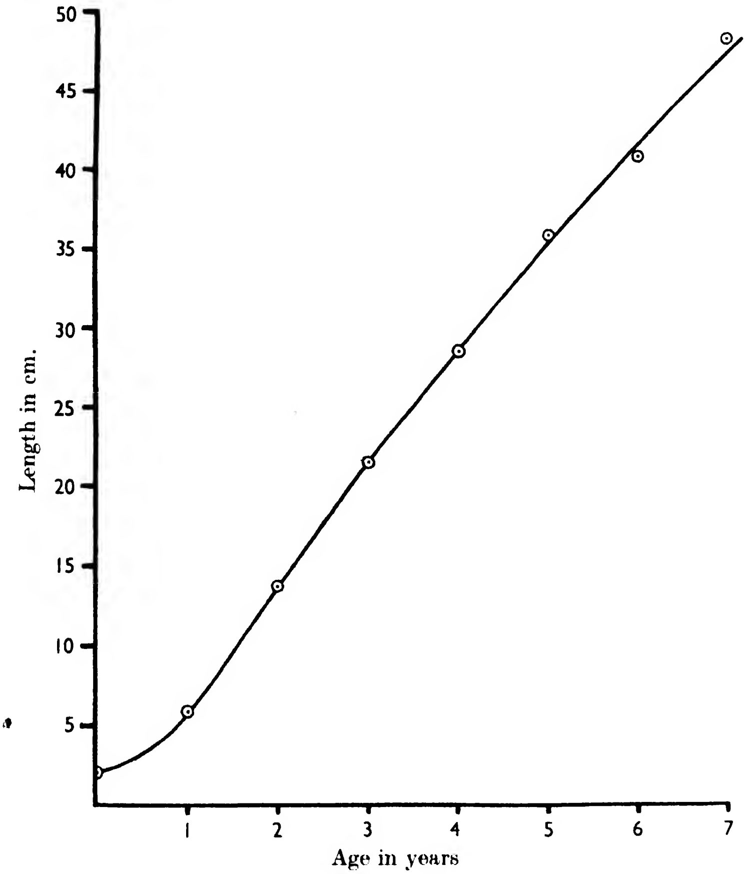

Fig. 1. The mean length of Windermere trout plotted against age.

examples from more peaty lakes may be quoted. In Lough Atorick, a peaty lake in the west of Ireland, Southern (1935) found that while the mean length of the trout after two years was 13·4 cm., after four years it was only 19·7 cm. In Three Dubs Tarn, a small peaty lake near Windermere, it was found that the trout grew to 17·3 cm. in two years, but when four years old were only 23·8 cm. in length. In these two lakes the total growth made during the third and fourth years is only 6·3 and 6·5 cm. respectively, while in Windermere the mean growth over these two years is 14·8 cm.

Observations showed that very few trout under about 12 cm. in length were to be found in the lake, and it was known that the great majority of adult fish entered the tributaries of the lake to spawn. Therefore it was considered probable that the young fish remained in the streams for a few years before descending to the lake. It was decided to examine the scales of the trout to see whether the change from stream life to lake life had any effect on the growth which would appear on the scales. The scales of nearly all fish showed a sudden well-marked increase in the growth rate at some point during the first three years. This effect is almost certainly due to the entry into the lake. Hence it is possible by examining the scales to determine at what age the fish entered the lake. This was done for a sample of 191 fish, and it was found that 12 % entered the lake after one year, 76 % after two years, and 12 % after three years.

Table 2. *The mean growth rates of trout entering the lake at different ages*

	Length in cm. after			
Age at migration	1 year	2 years	3 years	4 years
1 year	7·0	17·7	24·6	33·0
2 years	5·6	13·4	21·6	31·1
3 years	4·4	10·6	18·2	26·0

The mean growth rates of fish which migrated after one, two and three years have been worked out separately and are given in Table 2. The fish which migrated after one year had grown faster during their first year than the others, and those migrating after two years had grown faster during their first two years than those migrating after three years. This effect is well known in salmon and sea-trout.

From this it follows that since all the fish in the one-year class must be first-year migrants, and those in the two-year class must be first- or second-year migrants, these fish should show a higher average growth rate than those in the higher age classes which include the third-year migrants. Also, the fish in the one-year class should show a higher growth rate than those in the two-year class. This, as well as the selective action of the net, will tend to produce the more rapid growth which Table 1 shows to occur in the one- and two-year classes. Since the width of a circulus depends on the rate at which the fish is growing when the circulus is formed, an examination of the circuli at the edge of a scale should show whether the fish was making slow or rapid growth at the time it was caught. If this is done for fish caught at all times of the year it should be possible to determine how far the alternation of slow and rapid growth is a seasonal effect.

Table 3 shows that there is a definite seasonal effect and that in both years 76–100 % of the fish are showing rapid growth during the period May to August, while during the winter months the percentage showing rapid growth drops to a low figure. This clearly shows that rapid growth is typically a summer effect; although some fish show rapid growth on their scales during the winter,

probably due to two causes. First, it is possible that there is an overlap between the rapid growth periods of different years, i.e. in some fish the period of slow growth commences early and ends early, while in other fish it only begins late in the winter. Some fish of the first type will have recommenced rapid growth before some of the second type have entered the slow growth period. Consequently, at all times of the year, some fish will be making rapid growth.

Table 3. *The percentage of fish showing rapid growth in each two-month period: also the number of circuli in the outer annulus, the results for wide and narrow circuli being given separately*

	1933	1934						1935				
Time	Nov.–Dec.	Jan.–Feb.	Mar.–Apr.	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	Mar.–Apr.	May–June	July–Aug.	Sept.–Oct.
No. of fish	26	6	35	33	1	9	67	70	66	76	23	26
% showing rapid growth	35	13	51	76	100	0	22	36	61	97	78	54
Mean no. of wide circuli in outer annulus	5·4	3·5	3·9	4·3	5·0	—	12·0	6·1	4·8	7·2	11·0	7·7
Mean no. of narrow circuli in outer annulus	7·2	7·2	6·6	2·1	—	4·9	7·9	9·9	9·7	4·0	4·0	7·8

Close examination of the scales also suggests another explanation. In some fish a wide band of wide circuli is interrupted by one heavy or irregular line. Possibly this means that during the winter the fish made no growth at all and no band of narrow circuli was laid down. If that fish had been captured during the winter and its scales examined, the edge of the scale would have been found to consist of wide circuli. It is, therefore, likely that some at least of the fish found to be showing wide circuli during the winter are of this type.

Table 3 also shows for each two-month period the average number of wide or narrow circuli in each type of outer annulus. For convenience annuli composed of wide and of narrow circuli will be referred to as "wide" and "narrow" annuli respectively. Fig. 2A shows graphically the variation over the period of this investigation in the number of circuli in outer annuli of the "wide" type; while Fig. 2B shows the variation over the same period in the percentage of fish in which the outer annulus is "wide". In both years the maximum number of circuli occurs rather after the maximum percentage of fish with a "wide" outer annulus. This is to be expected since, while the number of rapidly growing fish decreases, those which are still growing rapidly will be adding to the width of their outer annulus, and the mean number of circuli in it will continue to increase.

After the maximum is passed the number of circuli in the "wide" annuli decreases gradually, and not abruptly; and in two cases the decrease begins well before the percentage of slow growing fish has reached its maximum. This

indicates that the fish with wide circuli at the edge of the scale during the winter are not entirely those which have stopped feeding. If this were so the

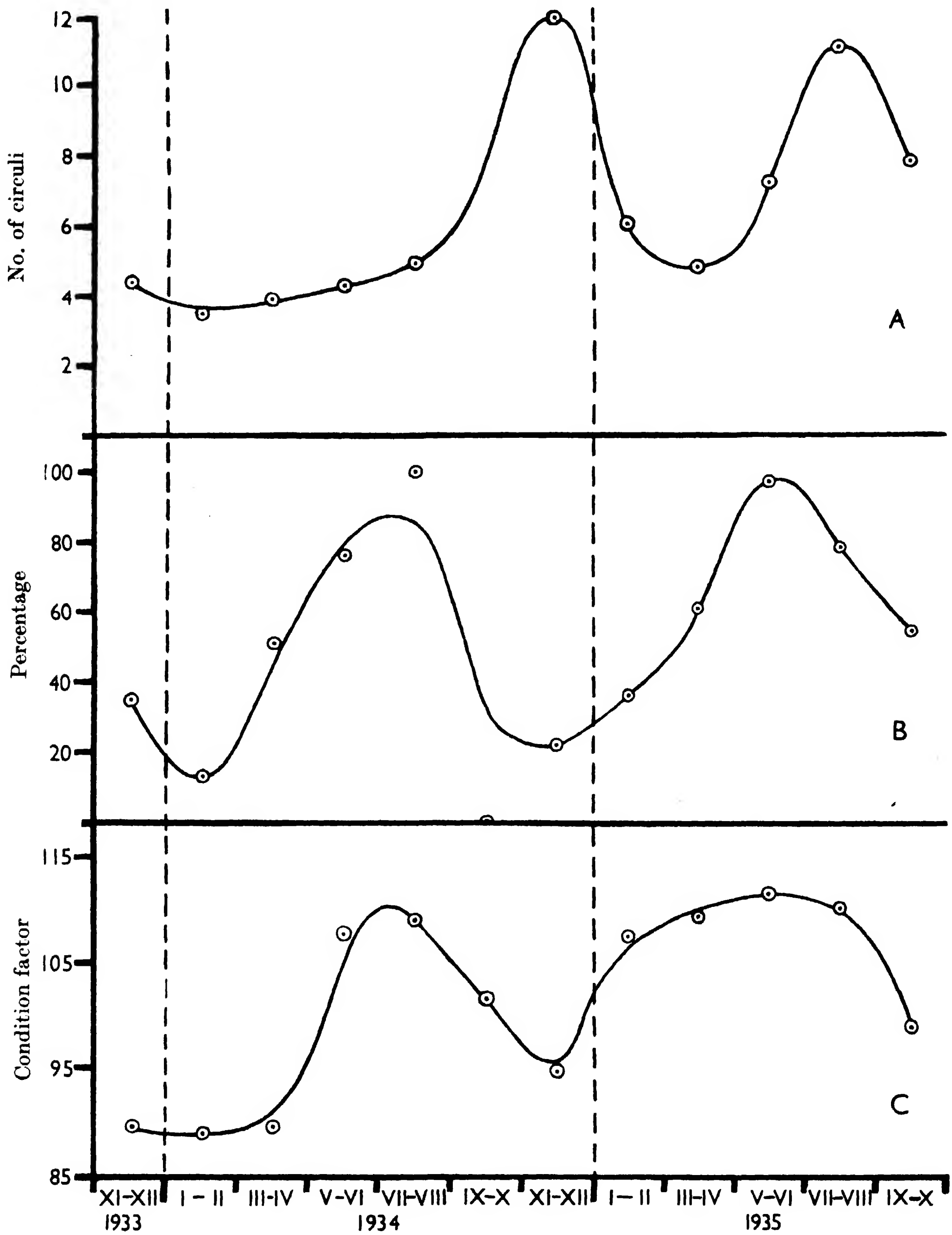

Fig. 2. The following plotted for each two-month period during the investigation. A. The mean number of circuli in "wide" outer annuli. B. The percentage of fish with "wide" outer annuli. C. The condition factor.

width of the annuli of wide circuli in those fish showing rapid growth would remain constant at a high value all through the winter and would fall abruptly

when rapid growth started again in the spring. Similarly, the number of circuli in "narrow" outer annuli reaches a maximum after the percentage of fish with outer annuli of this type has done so (Table 3).

Further information concerning seasonal growth has been obtained by the marking of fish. At various times about 200 trout were captured in the lake, marked and liberated. Before liberating the fish, scale samples were taken from them, and they were weighed and measured. The mark used was a numbered silver label, 9 by 3·5 mm., which was attached by a silver wire to the base of the dorsal fin. If these marked fish were recaptured later they were again measured and, in most cases, a further scale sample was taken. Thus it is possible to determine what has been added to the scales during a known period, and also what growth the fish has actually made during this time.

Excluding fish which were recaptured within three weeks of marking, 32 recaptures have been made, including three fish which were recaptured twice (Table 4). If the increase in length per day is compared with the period during which the fish were under observation, it will be seen that in general the fish which had a period falling largely in the months March to June show a higher rate of growth than the others. For all fish the mean date of the period between marking and recapture has been calculated, and for sixteen fish this date falls in the months February to July, and for the other sixteen in August to January. The mean rate of growth of the first series is 0·0211 cm. per day, while that for the second series is 0·0113 cm. per day. This provides direct evidence, as distinct from that deduced from the scales, that the trout tend to grow faster in the spring and early summer months.

The data about growth made by the scales of the recaptured fish support the view that the alternation between rapid and slow growth shown by the scales of nearly all fish may take place at different times of the year in different individuals. Nos. 112 and 119 were markedwithin a few days of each other and recaptured on the same day, and yet one had added wide circuli and the other a narrow circulus. Also, of the other fish marked in November, 107, 13, 16, 9 added narrow circuli first after they were marked, while 17, 27, 25 added wide circuli first. Comparison of other groups of fish marked at about the same time of year shows other similar cases. This strongly suggests that the overlap theory put forward to account for the wide circuli shown by some fish during the winter may be correct.

It is extremely probable that the same factors which cause a fish to grow fast will also cause it to be in good condition, i.e. its weight will be large in relation to its length. In order to get a numerical value for the condition of a fish, an expression must be used which contains the weight and length and is independent of the size of the fish. The simplest expression of this type would be in the form of W/L^n. If it is assumed that the specific gravity and the shape of the ideal fish remains constant throughout its life, then this expression becomes W/L^3. In the case of some fish, however, there is a progressive change in shape

Table 4. *The history of the marked trout which were recaptured. Lengths in cm.*

No.	Date when marked	Date when recaptured	Length when marked	Increase in length	Increase in length per day	Growth of scales
21	29 Nov. 1933	5 Jan. 1934	24·8	0·6	0·014	No data
101	15 Nov. 1934	15 Jan. 1935	27·4	1·2	0·020	No growth
140	15 Nov. 1934	22 Jan. 1935	22·8	0·6	0·009	No growth
112	23 Nov. 1934	22 Jan. 1935	24·8	1·3	0·022	Two wide circuli
119 (1)	28 Nov. 1934	22 Jan. 1935	21·6	0·6	0·011	One narrow circulus
147	23 Nov. 1934	28 Feb. 1935	28·7	1·2	0·012	No growth
107	15 Nov. 1934	14 Mar. 1935	29·9	1·3	0·011	Two narrow circuli
224	29 Nov. 1935	14 Mar. 1936	22·8	1·4	0·013	No growth
22	25 Nov. 1933	27 Mar. 1934	22·8	1·4	0·011	No growth
17	25 Nov. 1933	27 Mar. 1934	24·2	0·6	0·005	One wide circulus
13	25 Nov. 1933	27 Mar. 1934	22·8	1·9	0·016	Four narrow circuli
27	25 Nov. 1933	27 Mar. 1934	24·2	0·6	0·005	Three wide circuli
16	25 Nov. 1933	8 May 1934	24·2	3·8	0·023	Five narrow and three wide circuli
18	25 Nov. 1933	2 June 1934	26·2	3·1	0·016	No data
25	26 Nov. 1933	3 July 1934	31·2	0·6	0·003	Four wide circuli
9	25 Nov. 1933	9 Dec. 1934	21·6	12·1	0·031	Three narrow, eleven wide, ten narrow circuli
51	25 Jan. 1934	27 Mar. 1934	26·7	0·0	0·000	No growth
165	28 Jan. 1935	17 May 1935	29·3	1·0	0·009	No data
152	22 Jan. 1935	18 May 1935	20·9	2·7	0·023	No data
119 (2)	22 Jan. 1935	23 May 1935	22·2	3·5	0·029	Six wide circuli
185	26 Mar. 1935	25 Apr. 1935	25·4	0·6	0·020	Three narrow circuli
186	26 Mar. 1935	21 May 1935	23·5	1·5	0·027	Six wide circuli
73	27 Mar. 1934	2 June 1934	32·4	0·7	0·010	No data
92 (2)	14 Mar. 1935	18 July 1935	38·2	7·5	0·059	Five wide circuli
195	25 Apr. 1935	27 June 1935	27·5	1·7	0·019	No data
207	23 May 1935	12 June 1935	22·8	0·7	0·035	No data
205	21 May 1935	17 June 1935	25·6	0·2	0·007	No data
100	8 May 1934	10 Jan. 1935	36·3	4·4	0·019	Three narrow, three wide circuli
92 (1)	8 May 1934	14 Mar. 1935	35·7	2·5	0·008	Four wide, four narrow circuli
211 (1)	17 June 1935	18 July 1935	27·7	0·8	0·026	No data
211 (2)	18 July 1935	21 Aug. 1935	28·5	0·5	0·015	No data
269	18 July 1935	19 Sept. 1935	20·4	0·6	0·010	No data

during life so that in order to get an expression for normal condition which is independent of size, values of n must be used which differ slightly from three. The appropriate value of n may be determined for any sample of fish by plotting for each individual fish the logarithm of its weight against the logarithm of its length. If the relation between length and weight is of the type postulated then the points will lie about in a straight line whose gradient is n. This has been done for the trout examined during this investigation, and it has been found that there is no justification for giving n any value other than 3 in the case of Windermere trout.

All the trout which have been caught have been measured and weighed and their condition factor calculated. Measurements being made in centimetres and grams, it is found that the resulting value for the condition factor is in most cases of the order of 0·01. For convenience this figure has been multiplied by

10^4, and therefore the formula used in determining condition is $10^4 W/L^3$, and the resulting value is of the order of 100.

Since it was found that there are seasonal changes in the growth rate of the trout, the figures for condition factor were tested for the same effect. The result is shown in Table 5, and is expressed graphically in Fig. 2c. Fig. 2 shows that there is a clear correspondence between the average value of the condition factor and the rate at which the fish are growing. Both are at their maximum in summer and at their minimum in winter. Detailed comparison shows that the correspondence is even closer than this. In the winter 1934–5 both condition factor and rate of growth began to increase about the end of November while in the previous winter the increase did not begin until February or March. This suggests that there is a close connexion between condition and rate of growth.

Table 5. *The mean value of the condition factor and its standard deviation for each two-month period*

	No. of fish	Mean condition factor	Standard deviation
Nov.–Dec. 1933	35	89·5	10·4
Jan.–Feb. 1934	11	88·9	8·5
Mar.–April 1934	32	89·5	9·6
May–June 1934	54	107·8	9·7
July–Aug. 1934	18	109·0	9·9
Sept.–Oct. 1934	12	101·5	9·2
Nov.–Dec. 1934	68	94·7	8·3
Jan.–Feb. 1935	66	107·5	12·4
Mar.–April 1935	73	109·2	14·2
May–June 1935	86	111·5	9·0
July–Aug. 1935	24	110·1	7·6
Sept.–Oct. 1935	23	98·9	6·2

One other seasonal change shown by the fish may be considered at this point; this is a change in habitat. As already stated, the fish collected in the course of this investigation were caught in shallow water by means of a seine net. In Table 6 the results obtained with this net during the period 1 November 1934 to 30 October 1935 are tabulated. In the last four months there is a decided decrease in the average number of fish caught in one draw of the net. In the previous year netting was carried out less regularly, but a similar effect was also observed. Since it is unlikely that there was any significant decrease in the efficiency of the netting at this time, these results imply that there were fewer fish in the littoral region of the lake during the period July to October than during the rest of the year. But the trout do not leave the shallows entirely, being approximately one-third as numerous here at this time as they are in the winter and spring months. It is also known from the experience of men fishing for char in the lake that trout are not uncommon in the deep water away from the shore during the whole of the fishing season, March to October inclusive. It appears, therefore, that the trout do not perform a complete migration

between deep and shallow water, such as that made by the perch (Allen, 1935), but that they are at all times distributed between the deep and shallow water, and that there is a seasonal variation in the proportions occupying the two habitats.

Table 6. *The results of netting operations during the last twelve months of the investigation*

	No. of draws made	No. of fish caught	Average no. of fish per draw
Nov. 1934	12	69	5·7
Dec. 1934	3	10	3·3
Jan. 1935	12	58	4·8
Feb. 1935	11	23	2·1
Mar. 1935	16	34	2·1
April 1935	11	27	2·5
May 1935	12	46	3·8
June 1935	15	32	2·1
July 1935	16	18	1·1
Aug. 1935	16	9	0·6
Sept. 1935	10	11	1·1
Oct. 1935	8	9	1·1

Unfortunately it is not yet known whether individual fish move frequently from one habitat to the other, or whether they remain for long periods in either deep or shallow water and only occasionally move from one to the other. Only one trout which was marked in shallow water has been recaptured in deep water, but when it is considered that no netting has been done in deep water, and that angling takes place much more intensively in shallow water than in deep, this cannot be taken to indicate that only a small proportion of marked fish ever move to deep water. Since this particular fish was marked on 22 January 1935, and was recaptured on 18 May 1935, it appears that there is some movement between shallow and deep water at other times than that needed to account for the decrease in the number of trout in the littoral region during late summer. Thus it is probable that there is some interchange of fish between deep and shallow water throughout the year, but there is no evidence at present as to the frequency of this movement by individual fish.

It is not possible, therefore, to determine whether the falling off in growth rate and condition in the late summer is typical of all fish, as it would be if fish are moving frequently between deep water and the littoral region. If, on the other hand, there is only an infrequent movement, the fish captured at this time are those which are now definitely inhabiting the littoral region, and therefore the decreases observed apply only to these fish, and not to the whole population. The fact that there is no marked discontinuity in the growth and condition curves at the time when the fish again become abundant in the littoral region rather suggests that the results are applicable to the population as a whole, and therefore that there is a frequent interchange between deep and shallow water.

3. Food

The nature of the food of a fish is controlled first by what is available and secondly by the behaviour of the fish. The results obtained from the observations on the food of the trout in Windermere may be considered in relation to these two effects. The nature of the food varies very greatly at different times of the year. In Table 7 the percentage which the most important organisms were found to make up of the total food is recorded for each month. The percentage composition of the food varies greatly from month to month, and the year may be divided into three periods, in each of which the food of the trout is composed of a particular type of animal:

(*a*) October–February. During this period trout feed principally upon the permanent bottom fauna, i.e. Molluscs and Crustacea.

(*b*) March–July. During this period the trout feed largely upon the temporary bottom fauna, i.e. insect larvae and pupae. This period merges gradually into the next.

(*c*) May–September. During this period the trout feed largely upon terrestrial insects taken at the surface of the water.

Table 7. *The percentage composition of the food of the trout during each month*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Permanent bottom fauna:												
Asellus	15·1	16·1	1·2	8·4	3·7	—	1·2	—	0·7	1·4	53·7	65·6
Gammarus	70·5	41·2	12·1	8·1	25·3	4·0	0·6	—	10·2	19·4	17·5	29·4
Limnaea	3·9	23·7	7·7	6·4	1·6	0·9	11·2	3·7	3·6	32·7	3·9	—
Total	94·0	83·7	23·3	23·6	30·8	17·7	31·8	4·3	14·9	62·6	77·4	95·7
Temporary bottom fauna:												
Chironomid pupae	—	0·4	53·8	2·0	1·6	—	0·3	0·5	0·2	—	—	—
Nemura nymphs	0·2	2·9	6·0	30·7	3·7	—	—	—	—	—	0·1	0·5
Leptocerus larvae	0·5	0·4	0·8	4·8	15·1	37·1	36·2	—	2·4	2·5	0·3	0·3
Char eggs	—	—	—	—	—	—	—	—	—	—	13·0	—
Total	4·5	14·6	73·8	52·2	22·6	41·4	38·7	2·1	11·4	7·7	20·8	4·3
Surface food:	—	0·7	1·7	21·5	52·5	32·2	25·0	93·1	73·4	1·7	1·5	—

The changes in type of food taken do correspond to changes in the type of food available. The permanent bottom fauna is available throughout the year and is actually most numerous during the winter months (Humphries, 1936). The temporary bottom fauna is numerous during winter and spring, but during the winter most of the individuals are of small size and so this class only forms a suitable source of food during the spring months. Owing to the emergence of insect imagines the temporary bottom fauna is comparatively small during the summer. The third class of food, adult insects, is only available during the summer, but it appears that as soon as it becomes sufficiently numerous the trout feed almost exclusively upon it. That this is so was shown by the fact that in 1935, when, owing to suitable weather, adult insects were numerous from the end of April onwards, trout fed on the surface from this time onwards; while in 1934 surface feeding did not become frequent until the middle of June.

Further, it appears that throughout the summer there is a well-marked daily change between surface feeding and bottom feeding. This is shown by Table 8, which compares the percentage of surface food found in fish caught before and after 7.30 p.m. B.S.T. for each of the summer months. It seems that, with the exception of September when the trout are for a time feeding almost entirely on the surface, the percentage of food taken on the surface is much higher during the day than it is in the evening. Since the number of adult insects which are on the wing and hence liable to fall on the water decreases considerably in the late afternoon and evening, it is very probable that here again it is the quantity of surface food available that determines the type of food taken by the trout.

Table 8. *Comparison of the percentage of surface food in trout caught by day and by night*

	Before 7.30 p.m.		After 7.30 p.m.	
Month	No. of food animals	% caught on surface	No. of food animals	% caught on surface
Apr.	1066	28·1	308	1·6
May	1453	89·4	1964	16·1
June	551	36·6	575	1·7
July	308	25·7	15	6·7
Aug.	173	96·0	11	72·7
Sept. (first half)	183	97·3	356	99·7
Total	3734	80·4	3229	21·5

In the table, results are only given for the first half of September, since during this month the amount of surface feeding decreases very rapidly and it so happened that no fish were caught at night in the second half of the month. Thus, means for the month as a whole would be definitely misleading. As illustrating the rate at which surface feeding decreases during September, it can be stated that the percentage of surface food eaten by the nine fish caught in the second half of this month was only 15·9.

The results suggest that when all classes of food are available the trout will feed on the surface rather than on the bottom, and that, if no surface food is present, they will feed on the temporary bottom fauna rather than on the permanent bottom fauna. Schechtel (1927) has also observed that when surface food is sufficiently abundant, the trout in the Tatrasee feed on it in preference to other kinds.

Table 7 also shows that within these main variations in the type of food, definite seasonal changes also occur in the species of the bottom fauna eaten. The following summarizes the main points:

November–December. The principal food is *Asellus*, with a smaller number of *Gammarus*.

November. Towards the end of this month the char spawn on the shore of the lake, and at this time almost every trout caught in the parts of the lake where the char have been spawning has been found to be feeding almost exclusively on char eggs.

January–February. The number of *Asellus* eaten decreases, and *Gammarus* becomes the principal food, while *Limnaea peregra* becomes of increasing importance towards the end of this period. Whether there are corresponding changes in the fauna does not appear to be known.

March–April. At the end of March or the beginning of April there is a short period during which the imagines of *Endochironomus dispar* emerge in large numbers, and during this time the trout feed freely upon the pupae as they ascend to the surface.

April. The nymphs of *Nemura* form an important food. This is very probably correlated with the large size and increased activity of these nymphs just before hatching.

May–July. The larvae of *Leptocerus* now form the characteristic food. The causes of their prevalence in the food at this time are probably the same as those applying to *Nemura* in the previous month.

July–September. This, as already mentioned, is the period in which the trout feed almost entirely on the surface.

As already noted, it is probable that, particularly during the latter part of the summer, a large proportion of the trout are living not in the littoral region but in deep water away from the shore. Therefore surface food cannot strictly be regarded as the typical food of the trout at this time, although it is almost the sole food of those fish which are in the littoral region. Very few fish have been obtained from deep water, but those which have have been found to be feeding on the Crustacea of the plankton and on chironomid pupae. It is probable that the latter were taken as they rose to the surface to hatch.

The figures in Table 7 suggest that the percentages which the most important food animals make up of the food are probably very much greater than are their percentages in the fauna at the same time, i.e. that the fish are performing a definite selection in their feeding. In order to investigate this effect further it was decided to assume that all fish which contained more than 60% of one food animal were selecting food. Applying this test to 180 trout, which all contained ten or more food organisms, the results given in Table 9 were obtained. In addition to the 65% which thus appeared to be selecting a further 6% could have been regarded as selecting two food animals. An arbitrary criterion had also to be used to determine which fish had been selecting two animals. This was taken to be the two species together making up at least 90% of the food, and neither species being less than 30%. As it is very

Table 9. *The numbers and percentages of trout selecting different food animals*

	Numbers		Percentages	
Fish not selecting	—	52	—	29
Fish selecting *Gammarus*	33	—	18	—
Fish selecting *Leptocerus*	25	—	14	—
Fish selecting *Limnaea*	14	—	8	—
Fish selecting *Asellus*	13	—	7	—
Fish selecting *Nemura*	7	—	4	—
Fish selecting Char eggs	5	—	3	—
Fish selecting other animals	20	—	11	—
Total fish selecting one animal	—	117	—	65
Total fish selecting two animals	—	11	—	6
Total	—	180	—	100

unlikely that any of the food animals make up anything like 66 % of the fauna, it appears from the table that it is very probable that selection does occur. This hypothesis is strengthened by the fact that on several occasions different fish caught at the same time and place were found to be selecting different foods. Southern (1935) records that out of 80 trout from Lough Derg which contained food 59 were found to have been feeding predominantly on one food. The criterion of dominance is not stated.

It has been shown (Allen, 1935) that in another carnivorous fish, the perch (*Perca fluviatilis*), there are changes in the nature of the food with the size of the fish, and this effect has also been described in other species. With perch in Windermere the small fish feed on zooplankton, the medium fish on the bottom fauna, and the large fish upon smaller fish of the same and other species. The data obtained for the trout have also been examined for this effect. It has been found that very few trout feed upon plankton; this is very probably because the majority of fish do not enter the lake until they are too large to find the small organisms composing the plankton a satisfactory diet. (Out of 339 trout stomachs examined only one contained plankton in any quantity.)

As has been seen, the majority of the trout in Windermere are in the insect feeding stage, although a few trout of all sizes have been found to contain small fish (usually minnows). It does appear, however, that the very large trout over 40 cm. in length feed largely on smaller fish. Only five fish of this size were examined, but four of these had been feeding on other fish which were between 7 and 23 cm. in length; while out of 25 fish between 35 and 40 cm. in length, only five had been feeding upon fish, and only one upon fish over 5 cm. in length. Below 35 cm. no trout had been eating fish over 5 cm. in length, and very few had been eating smaller fish. Thus there seems to be a tendency for fish over 40 cm. in length to feed upon other fish (usually 10–15 cm. in length) while trout below 40 cm. rarely eat fish. But as these large fish are very rare, changes of food with size are quantitatively negligible in Windermere trout.

Table 10. *The amount of food found in the stomachs of trout in each month*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Wt. of food as percentage of wt. of fish	0·30	0·13	0·14	0·17	0·26	0·16	0·07	0·12	0·12	0·10	0·26	0·12
Mean no. of animals per fish	94	23	70	35	67	27	10	28	42	26	88	66

Observations have also been made on the amount of food found in the stomachs of the trout (Table 10). This gives for each month the mean dry weight of the food expressed as a percentage of the live weight of the fish, and also the mean number of food animals found in one stomach. Owing to the wide range of individual variation it is doubtful whether there are any significant differences between the figures for different months, although there may be a tendency for the fish taken in the months July to October to contain less

food than those taken in the other months. Since there is probably a considerable increase in the rate of digestion with increase of temperature, as has been shown for other species of fish (Scheuring, 1928), there may actually be an increase in the amount of food eaten during the summer months. This is in accordance with the increase in growth rate already shown to occur at this time.

4. POPULATION

From the data that have been obtained in the course of this work it is possible to make some estimate of the size and composition of the trout population of Windermere. From the recoveries of marked trout it is possible to gain some idea of the efficiency of the seine net used in catching them. It has been found that a large proportion of the fish remain for a considerable time (up to 18 months) in one place. Analysis of the recaptures of these fish shows that if a fish is recaptured at all, it is on the average recaptured in the third subsequent draw made in the place where it was liberated, i.e. the net captures one-third of the trout in the area which it covers. From Table 6 it seems that during the part of the year when the trout are most numerous in shallow water the average catch in one draw of the net is three trout. It follows that the average trout population of the length of shore covered by the net is nine. Since this length of shore is approximately 40 m. and the total shore line of the lake is 40 km., the trout population of the littoral region of the lake is of the order of 9000.

Certain corrections must be applied to this result. Table 1 shows the age composition of the sample of fish examined. Very few one-year-old fish were caught, about equal numbers of two-year-old and three-year-old fish, and rapidly decreasing numbers of fish in later years. Table 1 shows that the average fish does not reach the length of 20 cm. until late in its third year. But the net used allowed some fish under 20 cm. to escape, so that a considerable proportion of the two-year-old fish in the area enclosed by the net would escape through the meshes before the net was drawn on shore; and nearly all the one-year-old fish present would escape in the same way. Therefore the actual percentage which one- and two-year-old fish make up of the total population will be greater than the percentages in Table 1.

When the proportion of fish entering the lake at various ages is considered, and the probable rate of mortality, it appears likely that the actual number of two-year-old fish inhabiting the littoral region of the lake is between one-and-a-half and twice the number of three-year-olds in the same region. The proportion of one-year-old fish, although higher than is indicated by Table 1, is probably still small since the percentage of trout entering the lake as yearlings has been shown to be small. It seems likely that about half the trout population of the littoral region consists of fish in their third year (i.e. fish which have completed two years), about half the remainder are fish in their fourth year,

the rest being distributed between one-year fish, and fish more than four years old.

The estimate previously reached of the total number of fish in the lake was 9000, but, as stated, this did not make any allowance for the one- and two-year-old fish which escaped the net. The three-year-old fish cannot escape through the net and would be estimated accurately. They made up one-third of the sample obtained, and since the figure for the total population reached on this sample was 9000, it is probable that the number of three-year-olds in the lake is about 3000. We have already seen that actually the three-year-olds probably form one-quarter and not one-third of the total population, and therefore it is likely that the total trout population of the littoral region of the lake is of the order of 12,000.

5. Summary

1. The mean annual rate of growth of trout in Windermere remains almost constant throughout life, and is about 7 cm. a year.

2. The majority of the young fish enter the lake from the streams when two years old, although some enter after one and after three years.

3. The fish entering the lake when one year old are larger at the same age than those which migrate later. Similarly those which migrate when two years old are larger at the same age than those which migrate after three years.

4. The percentage of fish growing rapidly, as judged by the width of the circuli at the edge of the scale, is at a maximum (75–100 %) in the summer, and at a minimum in winter. Two possible causes of the rapid growth shown by about 25 % of the fish in winter are put forward.

5. The condition factor of the fish shows seasonal variations closely parallel to those shown by the percentage of fish growing rapidly.

6. The trout show well-marked seasonal variations in the nature of the food eaten. There are three main periods: in October to February the trout are feeding on the permanent bottom fauna, in March to July on the temporary bottom fauna, and in May to September on the surface food.

7. There is little change in food with the size of the trout, except that fish over 40 cm. in length feed largely on smaller fish.

8. The trout population of the littoral region of Windermere is estimated to be 12,000; of which 50 % are fish in their third year, and 25 % fish in their fourth year.

REFERENCES

* Not verified in the original.

Allen, K. R. (**1935**). "The food and migration of the perch (*Perca fluviatilis*) in Windermere." J. Anim. Ecol. 4: 264–73.

Humphries, C. F. (**1936**). "An investigation of the profundal and sublittoral fauna of Windermere." J. Anim. Ecol. 5: 29–52.

Pearsall, W. H. (**1930**). "Phytoplankton in the English Lakes. 1. The proportions in the waters of some dissolved substances of biological importance." J. Ecol. 18: 306–20.

Schechtel, E. (**1927**). "Pokarm powietrzny u pstraga." Roczniki Nauk Rolniczych i Lésnych. 18: 1–15.

***Scheuring, L.** (**1928**). "Beziehungen zwischen Temperatur und Verdauungsgeschwindigkeit bei Fischen." Z. Fisch. 1928.

Segerstråle, C. (**1933**). "Über scalimetrische Methoden zur Bestimmung des linearen Wachstums bei Fischen insbesondere bei *Leuciscus idus* L., *Abramis brama* L. und *Perca fluviatilis* L." Acta Zoologica Fennica, 15: 1–168.

Southern, R. (**1935**). "Reports from the limnological laboratory. 3. The food and growth of brown trout from Lough Derg and the River Shannon." Proc. Roy. Irish Acad. 42, B: 87–172.

FLUCTUATIONS IN NATURAL POPULATIONS OF COLLEMBOLA AND ACARINA. PART 2

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(*With* 6 *Figures in the Text*)

CONTENTS

1. Introduction

In a previous paper (Ford, 1937) a quantitative census of Collembola (springtail) and Acarina (mite) populations inhabiting a community of the grass *Bromus erectus* near Headington Wick, Oxford, was reported for the period November 1935 to March 1936. Various censuses of similar populations, made in widely separated districts, showed fluctuations similar to those obtained in the Brometum community. It was suggested that although climatic changes initiated the increases in population density of these forms at the beginning of winter, the subsequent fluctuations could not be entirely accounted for by climate.

The present paper is concerned with a second census of the same community carried out from September 1936 to April 1937 and includes also certain confirmatory observations made in the following winter, 1937–8. A description of the habitat, lists of the species living in it and the techniques used in making counts, have already been given in the paper cited above. This second census has yielded further information on the course taken by the population fluctuations; on the changes, from year to year, in the composition of the community; on the changes, during population fluctuation, of the age distribution

of the springtail, *Pseudachorutes subcrassus* Tbg.; and on the relation between the spatial distribution of the community and population density. That an investigation of the distribution of the community within the habitat might give useful results had been suggested by an examination of some of the results of the first census and a method of sampling was devised to supply this information. Unfortunately, though successful in this direction, this method involved an inaccuracy not discovered till too late for adjustment. However, this inaccuracy was not sufficient to obscure the results and was adjusted in the partial third census of 1937–8. It also proved beneficial in yielding information on the behaviour of individual species which might otherwise have been overlooked.

I am greatly indebted to Prof. G. D. Hale Carpenter who allowed me to continue this work in the Hope Department of Entomology.

2. Sampling methods

It was desired, in addition to obtaining a figure for population density at each sampling date, to get some idea of the evenness, or otherwise, of the distribution of the fauna between the tussocks of *Bromus*. On each sampling date, therefore, nine samples were taken, in three groups of three each, each group being taken from the stock region of a single tussock (region A in Ford, 1937). This permitted measurement of variability both between and within tussocks. Extraction of the fauna was carried out on a battery of small Tullgren funnels and counts were made as formerly described. From 21 September until 23 November 1936 samples were taken at weekly intervals; from then until 21 December at two- or three-day intervals; from 28 December 1936 until 18 March 1937 at three- or four-day intervals; concluding with four sets of samples at weekly intervals in April 1937: in all comprising fifty sets of nine samples each. Throughout this paper population density is expressed as number of organisms per g. of dry grass.

Most estimates of density are somewhat arbitrary from the point of view of the organisms concerned. In this case a more appropriate measure would take into account the area of grass surface available for mite or springtail to walk over. By unfolding the covering layers on the grass stalks, between which these organisms live, we may get a rough estimate of the surface area of a gram of dry grass. Three such estimates were made, giving a mean value of 296 ± 33 sq. cm. per g. of dry grass. The greatest population density recorded in 1936–7 was 45·79 organisms per g. Allowing 0·25 sq. mm. as the area occupied by a stationary organism (a conservative estimate) then at the period of greatest density each individual has territory 2600 times its own area available to it. If in similar fashion, we allow 1 sq. yd. to be the area occupied by a stationary man, then we find that the population of the Brometum, at its greatest density, is rather less crowded than are the inhabitants of Belgium.

Temperature and relative humidity were recorded on instruments kept in a Stevenson screen near the sampling area. Fig. 1 illustrates the general weather record for September 1937 to April 1938. Temperature is based on the records obtained at Headington Wick, the remaining data being obtained from the Radcliffe Observatory, Oxford. It has been demonstrated (Ford, 1937) that the microclimatic conditions affecting the Brometum inhabitants differs considerably from external air climate and the above records are only intended to indicate changes in the latter. A more important index of climatic conditions affecting the Brometum community is obtained in the water content of the grass samples, found by determining the loss of weight taking place during the drying of the samples for extraction of the fauna. This is included in Table 4.

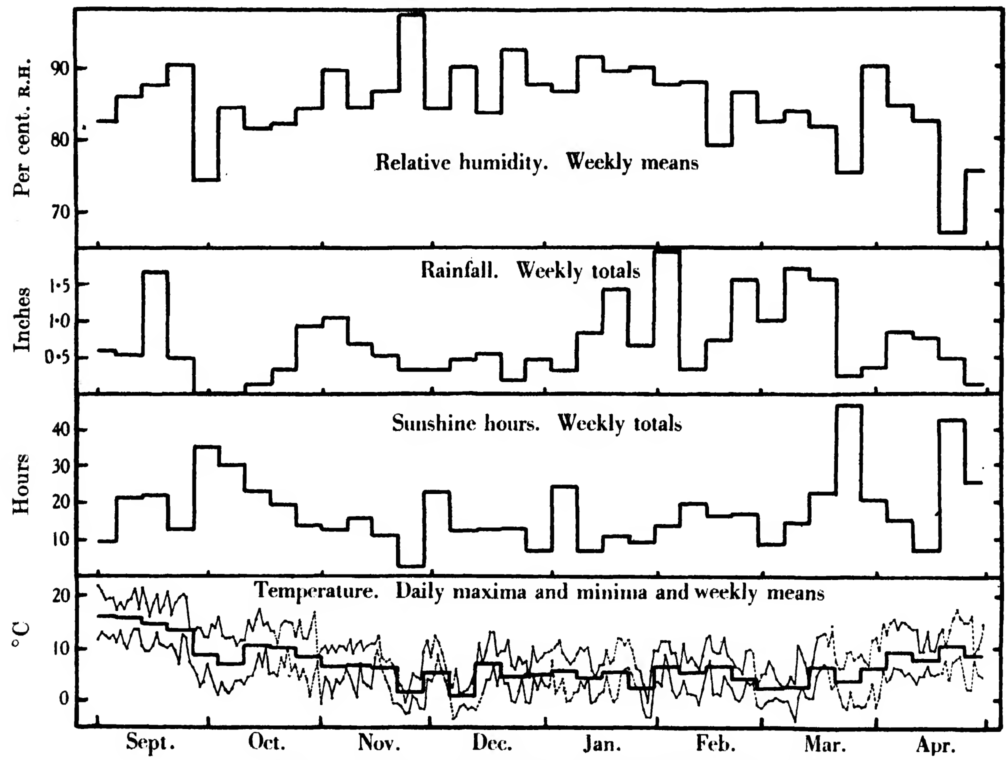

Fig. 1. Climate records, September 1936 to April 1937.

3. Composition of the fauna

Table 1 gives the average densities of the main components of the Brometum fauna in three successive winters, expressed as percentages of the total density.

The principal change was the great decrease in numbers of the springtail, *Pseudachorutes subcrassus*, following the winter of 1935–6.[1] This had the natural

[1] To test the possibility that this species had been affected by the process of sampling carried on in the Brometum, samples, totalling 18·4 g. of dry grass were taken on 8 February 1937, from a patch of *Bromus* which in the first year had yielded a high density of *P. subcrassus* but which had only been sampled twice. Nine individuals were obtained among a population of 601 organisms, thus showing clearly that the decline had been independent of the effects of sampling.

Table 1. *Percentage composition of whole fauna*

	Pseudachorutes subcrassus Tbg.	Other Collembola	*Hypochthonius pallidulus* Koch	*Asca aphidioides* Kram	Immature mites (excluding Trombids)	Trombidiformes	Oribatidae	*Eulaelaps stabularis* Koch	Other Acarina	Thrips	Other species
1935–6	57·5	2·1	8·5	8·6	3·0	5·6	5·3	1·4	1·4	4·7	1·8
1936–7	4·2	3·9	21·0	18·6	20·8	10·7	7·1	7·4	2·5	3·0	0·9
1937–8	0·4	3·9	26·3	6·7	26·8	16·5	4·6	10·2	1·5	2·0	1·1

effect of increasing the proportion of the population occupied by the other two predominant species, the mites *H. pallidulus* and *A. aphidioides*. The second of these species, however, showed a decrease in the third winter. This appears in Table 2, where the percentage composition of the Acarine fauna is shown.

Table 2. *Percentage composition of Acarine fauna*

	H. pallidulus	*A. aphidioides*	Immature mites (excluding Trombids)	Trombidiformes	Oribatidae	*E. stabularis*	Other Acarina
1935–6	25·1	25·3	9·0	16·6	15·7	4·2	4·2
1936–7	23·9	21·2	23·6	12·1	8·1	8·4	2·8
1937–8	28·3	7·3	28·9	17·9	5·0	11·0	1·6

This table, although giving only a partial analysis of the mite fauna, shows that definite alterations had taken place in relative densities of different species. Thus although the small Sarcoptiform species, *H. pallidulus*, continued to reach a high density, the Parasitiform *A. aphidioides* showed a decline; while the third most abundant species, the Parasitiform *E. stabularis* increased. Most notable, however, was the increase, between the first and second winters, of the proportion of immature forms (excluding Trombidiformes).

In addition to the changes in relative density of different species noted above, a marked alteration in the total density of the population of all species took place. An accurate comparison is not possible since the chief results of 1935–6 were obtained by a different technique and expressed according to the number of organisms per unit area. However, during part of that winter samples were also taken according to the present method. Between 24 January and 20 March 1936, parallel sets of samples taken by different techniques yielded average densities of 10,101 organisms per sq. m. and 29·2 per g. of dry grass. The ratio of these figures enables us to compare the population densities of 1935–6 with the two succeeding winters (Table 3). The average density given for 1937–8 is probably too high, as sampling was discontinued in January and thus did not include the whole period of the population decline. This remark applies to any other averages given for this winter later in the paper. Also the average density given for 1936–7 is probably slightly too low, for reasons to be discussed later.

Table 3. *Highest and average densities of the population of all species in three successive winters. (Organisms per g. dry grass)*

	Highest density		Average density	
	Including *P. subcrassus*	Excluding *P. subcrassus*	Including *P. subcrassus*	Excluding *P. subcrassus*
1935–6	85·4	36·3	36·8	15·9
1936–7	45·8	44·7	24·5	23·4
1937–8	44·4	44·1	29·0	28·9

Although it would be rash to postulate any causal connexion between the densities of population of the springtail *P. subcrassus* and the remaining species, Table 3 is certainly suggestive of such a connexion. Although as a result of the almost complete disappearance of this species in 1936–7 the highest density reached and the average density were both lowered, there was an increase in the density of the remaining population (mainly of mites), which was maintained at very nearly the same level in the following year.

4. Data for 1936–7

Table 4 summarizes the data from fifty sets of samples.[1] Each figure expresses the number of organisms per g. of dry grass and is the mean of nine samples. The four principal species are treated separately as above, while other species are grouped under appropriate headings.

In the last column of Table 4 is given the average water content of the samples, expressed as a percentage of their dry weight. From this table the data for population density of mites and for water content are shown graphically in Fig. 2. In this figure and in the table it is seen that their exists a partial correlation between some of the species and the water content of the samples. This is especially so with *H. pallidulus*, and the group of immature mites. With these species the samples showed a higher density when the grass was wet and therefore failed to give a correct value on dry days. It was eventually discovered that this was due to a fault in technique. In 1935–6 the sampling unit used was an area and from this all surface vegetation was removed, including the bases of grass leaves to the level of the roots, which lie from $\frac{1}{8}$ to $\frac{1}{4}$ in. below the soil level. In the smaller (weight) samples now under discussion the grass was cut off at the level of the soil, generally leaving about $\frac{1}{4}$ in. of grass stump untouched. On a previous occasion, when it was thought that the fauna of the grass might have retreated into the soil, examination of the soil had failed to yield any evidence of a downward movement. It was, therefore, necessary in the next winter (1937–8) to determine whether the mites retreated to the extreme base of the leaves during comparatively dry periods or whether the previously undertaken examination of the soil had been faulty.

[1] Space does not permit full publication of results, but a full copy of the original data is being deposited for reference at the Bureau of Animal Population, University Museum, Oxford.

Table 4. *Numbers of organisms per g. of dry grass, 1936–7, with percentage water content of samples*

Date	*P. subcrassus*	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites (excluding Trombids)	Trombidiformes	Oribatidae	*E. stabularis*	Remaining Acarina	Thysanoptera	Other species	% water content of samples (mean)
21 Sept.	0·25	1·30	—	6·06	1·32	1·18	2·98	1·10	0·35	1·65	0·23	188
28 Sept.	0·80	0·74	0·03	6·80	6·06	0·62	2·77	0·94	0·40	0·39	0·29	121
5 Oct.	0·44	0·32	—	7·51	6·60	1·01	1·11	0·67	0·31	0·05	0·56	93
12 Oct.	0·36	1·00	0·24	7·68	4·63	1·45	1·61	0·94	0·25	0·19	—	98
19 Oct.	0·61	0·34	0·14	8·47	1·40	2·34	1·31	0·80	0·22	0·59	0·42	84
26 Oct.	0·30	0·38	1·51	4·38	5·90	1·06	1·82	1·14	0·41	0·22	0·27	167
2 Nov.	0·77	0·41	3·18	4·70	11·18	1·17	4·35	1·20	1·96	0·55	0·70	241
9 Nov.	0·60	0·41	1·55	7·63	1·46	4·01	0·66	1·45	0·10	1·38	0·05	112
16 Nov.	1·20	1·21	3·67	4·57	6·65	3·99	1·18	0·60	0·14	0·23	0·08	117
23 Nov.	0·99	0·60	2·06	2·19	3·21	0·90	2·02	1·38	0·50	0·05	0·31	178
25 Nov.	1·05	2·26	11·95	3·45	5·18	5·55	1·43	1·92	0·64	0·57	0·20	163
27 Nov.	1·18	1·24	7·44	7·42	4·67	2·36	1·53	3·02	1·14	—	0·33	181
30 Nov.	2·03	1·19	11·98	6·01	7·19	3·16	1·98	2·95	0·60	1·85	0·60	138
2 Dec.	1·16	2·03	12·07	8·71	8·45	1·73	3·11	1·53	0·68	0·21	0·25	149
4 Dec.	0·75	1·08	6·36	5·61	3·69	3·12	0·35	1·66	0·22	0·33	0·43	88
7 Dec.	2·60	0·36	7·27	4·81	4·01	3·23	1·54	2·09	0·16	0·86	0·10	112
9 Dec.	1·63	0·86	10·26	3·72	3·16	2·56	1·72	1·27	0·75	0·76	0·25	194
11 Dec.	1·05	1·12	26·45	4·55	5·63	2·75	1·35	1·93	0·51	0·34	0·11	200
14 Dec.	1·00	0·61	17·06	4·65	6·32	2·72	1·24	1·96	1·48	0·84	0·38	310
16 Dec.	1·55	0·25	11·78	3·75	7·82	3·11	1·48	3·69	0·88	0·39	0·14	139
18 Dec.	1·96	1·77	6·42	6·49	5·60	5·02	2·36	2·82	0·60	0·59	0·33	180
21 Dec.	1·20	0·56	6·50	4·37	5·27	5·21	0·70	1·63	0·39	0·30	0·09	109
28 Dec.	1·32	0·22	3·21	4·81	7·99	6·86	1·73	2·92	0·28	0·50	0·24	128
31 Dec.	1·50	0·41	4·77	2·64	7·73	4·06	1·26	1·47	0·15	0·95	0·24	93
4 Jan.	2·66	1·35	6·70	4·19	4·59	2·51	1·90	2·33	1·26	0·43	0·43	106
7 Jan.	2·65	0·51	7·51	6·60	5·08	2·88	0·95	1·97	0·41	0·37	0·21	123
11 Jan.	1·71	0·13	6·66	6·06	4·50	2·78	1·40	3·58	0·50	0·60	0·24	130
14 Jan.	1·74	0·84	4·54	5·35	3·59	3·33	2·74	3·19	0·42	0·74	0·22	234
18 Jan.	2·24	2·86	11·69	2·99	15·95	3·35	3·03	1·70	0·73	0·75	—	318
21 Jan.	1·19	1·31	10·78	3·64	5·91	1·60	1·50	0·73	0·69	0·56	0·20	196
25 Jan.	2·06	1·19	3·04	2·99	6·70	2·55	3·19	3·02	0·45	0·59	0·17	230
28 Jan.	1·84	1·03	3·04	4·20	2·66	3·67	1·26	2·52	0·17	1·59	0·13	159
1 Feb.	0·51	1·60	3·08	4·83	3·16	3·87	1·27	2·50	0·14	0·27	0·10	107
4 Feb.	1·47	0·38	2·83	2·81	3·40	4·07	0·94	3·25	0·61	1·38	0·06	270
8 Feb.	1·01	2·93	9·75	2·30	4·10	1·56	2·96	2·92	0·54	1·11	0·16	237
11 Feb.	0·71	0·36	2·84	1·56	4·10	2·88	0·75	1·74	0·20	0·60	0·29	104
15 Feb.	0·93	0·88	1·97	4·02	5·70	3·74	1·42	1·48	0·75	1·25	0·16	143
18 Feb.	0·49	2·00	3·24	2·67	3·93	2·48	2·07	2·86	0·56	1·22	0·11	238
23 Feb.	0·37	0·98	1·94	2·27	4·38	1·93	1·09	1·33	0·81	1·61	0·12	112
25 Feb.	0·30	0·66	4·41	3·83	4·59	1·57	1·54	1·51	1·94	1·00	0·11	296
1 Mar.	0·68	1·36	3·20	5·13	2·15	2·08	0·65	0·72	0·49	1·20	0·37	145
4 Mar.	0·20	0·50	1·45	3·84	4·39	1·16	0·63	1·84	0·64	0·55	0·17	94
8 Mar.	0·49	0·43	1·97	2·65	7·26	2·82	0·93	3·58	0·50	2·16	0·06	174
11 Mar.	0·31	1·04	3·07	3·50	7·95	1·66	1·37	2·20	2·71	0·86	—	174
15 Mar.	0·23	1·20	0·71	3·99	2·59	1·88	1·16	1·38	0·38	1·08	0·23	82
18 Mar.	0·57	1·41	3·52	2·97	1·93	1·42	1·63	1·08	0·27	1·12	0·27	120
1 Apr.	0·19	0·14	0·38	2·05	2·36	0·78	0·89	0·19	0·31	0·86	0·05	86
5 Apr.	0·54	0·46	0·92	4·01	4·01	2·12	2·42	0·55	0·72	0·60	0·22	106
12 Apr.	0·14	0·36	0·19	4·76	2·42	1·53	1·07	0·32	0·35	0·30	0·25	95
19 Apr.	0·18	1·09	1·27	3·66	5·65	1·38	6·30	0·52	0·74	0·26	0·34	164
Means	1·03	0·95	5·13	4·56	5·08	2·61	1·73	1·80	0·61	0·74	0·22	156·5

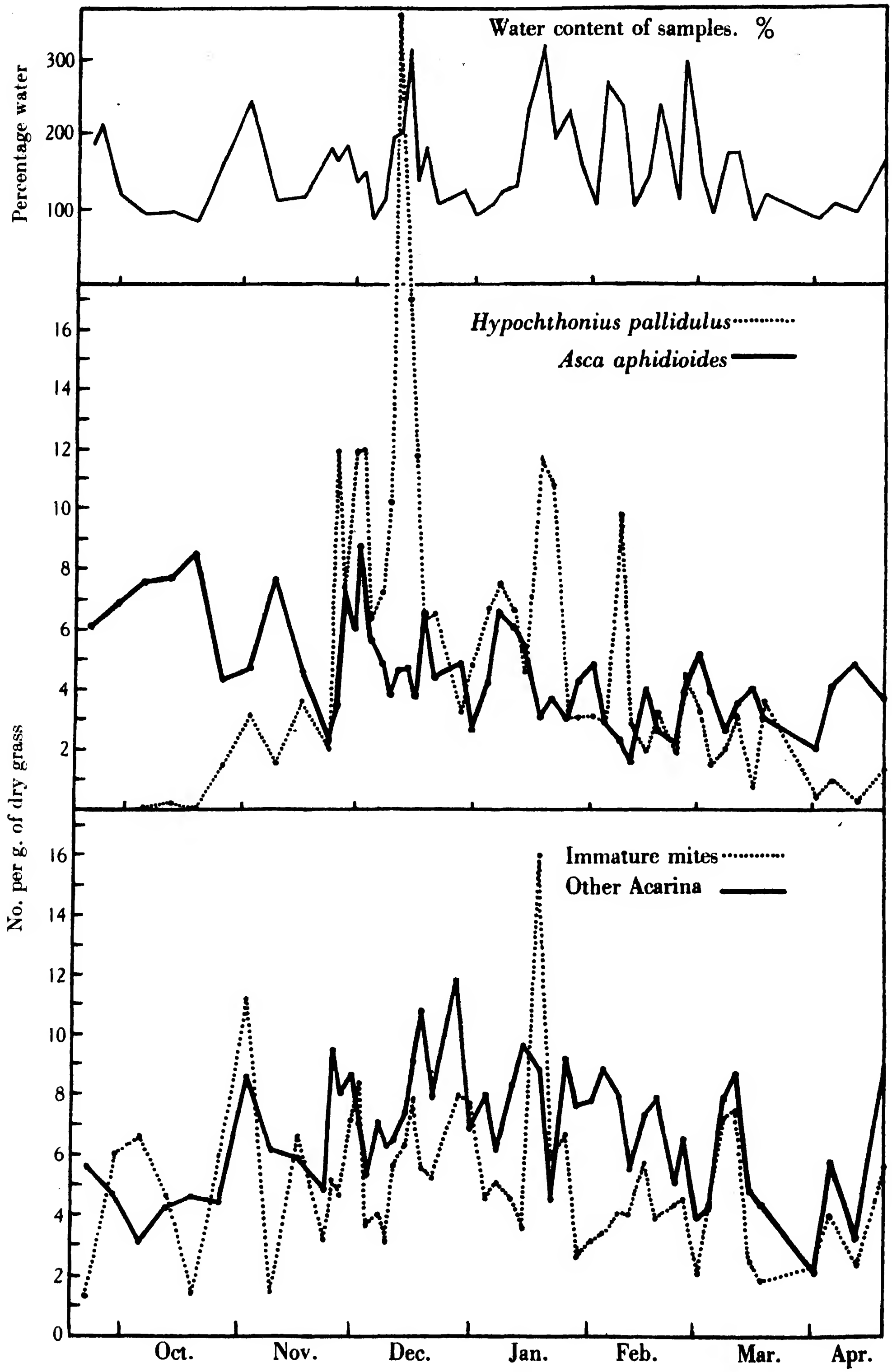

Fig. 2. Density changes in mite population, with water content of samples, 1936–7.

5. DATA FOR 1937–8

Circumstances did not permit frequent sampling in this winter but sufficient data were obtained to settle some of the points at issue in the previous season. Table 5 gives the results of sampling carried out as above, save that individual samples were taken, not in groups of three, but each from separate tussocks.

Table 5. *Number of organisms per g. of dry grass*, 1937–8, *with percentage water content of samples*

Date	*P. subcrassus*	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites	Trombidiformes	Oribatidae	*E. stabularis*	Remaining Acarina	Thrips	Other species	% water content
17 Oct.	—	0·03	0·07	1·92	2·05	3·10	0·18	1·12	0·03	0·24	0·03	—
7 Nov.	0·06	0·26	0·86	1·20	5·30	3·70	2·16	2·90	0·53	0·26	0·20	—
24 Nov.	0·11	1·19	14·26	1·98	8·63	4·35	1·58	3·49	0·29	0·32	0·29	204
1 Dec.	0·07	1·89	6·02	1·99	8·60	3·87	1·86	1·56	0·68	0·59	0·29	222
8 Dec.	0·05	1·80	8·41	2·92	9·48	3·18	1·44	3·18	0·26	0·98	0·31	197
15 Dec.	0·28	2·07	14·82	3·02	11·40	5·15	1·29	4·70	0·73	0·28	0·67	209
21 Dec.	0·23	0·63	9·49	1·71	8·92	6·49	0·91	3·30	0·23	1·02	0·40	260
30 Dec.	0·10	0·73	10·05	2·04	9·32	2·41	1·36	2·78	0·58	0·79	0·21	275
5 Jan.	0·11	1·65	7·35	1·81	7·35	7·39	1·86	4·31	0·58	0·64	0·27	248
13 Jan.	0·05	1·07	8·30	1·26	7·53	5·49	1·36	2·04	0·19	0·19	0·39	198
18 Jan.	0·05	1·07	4·05	1·68	6·93	7·67	0·74	3·25	0·65	1·07	0·60	176
Means	0·11	1·13	7·61	1·96	7·77	4·80	1·34	2·97	0·43	0·58	0·33	221

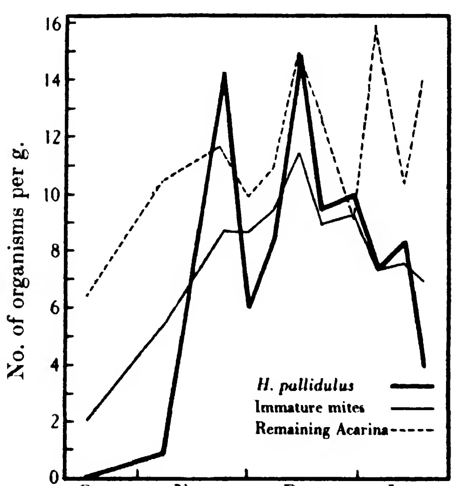

Fig. 3. Density changes in mite population, Oct. 1937–Jan. 1938.

Some of the data of Table 5 are shown graphically in Fig. 3. On each sampling date it happened that the water content of the grass was high and on no occasion as low as the average for the previous year. The *H. pallidulus* population follows a trend similar to that of the year before, with a peak on 15 December, evidently corresponding to that of 11 December in 1936, though not of so great a density. There is another peak on 24 November which has its counterpart between 25 November and 2 December in the previous year. Whether or not this peak is a true one must remain doubtful, since in 1936 the decline following it was correlated with relative dryness in the samples, though this was not so in 1937. In 1935 a similar decline was detected between 30 November and 29 December (approximately) in the *P. subcrassus* population, but not in that of *H. pallidulus*.

The comparative evenness of the data for the population of immature mites in Fig. 3 may be accounted for by the uniformly high water content of the samples. The combined data for the remaining Acarina (including *A. aphidioides*), however, are irregular and show a tendency to maintain a high density till later in the season, again as in 1936–7.

In addition to the samples treated above, three samples were taken on each date of the leaf bases of the *Bromus*, at ground level. These were extracted as usual and yielded the following results (Table 6).

Table 6. *Number of organisms per g., in leaf bases of* Bromus *at ground level*, 1937–8

Date	*P. subcrassus*	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites	Trombidiformes	Oribatidae	*E. stabularis*	Other Acarina	Thrips	Other species
24 Nov.	—	1·20	0·80	1·60	2·80	—	2·00	—	—	—	0·40
8 Dec.	—	0·65	0·78	1·04	15·20	0·78	1·43	0·39	0·26	—	—
15 Dec.	0·18	3·68	0·88	4·56	11·93	2·10	5·79	1·58	0·70	0·18	0·35
21 Dec.	—	0·65	1·52	2·39	11·75	2·83	3·91	1·30	0·43	—	0·22
30 Dec.	—	1·63	0·41	1·43	12·25	0·20	4·69	0·41	0·61	—	0·82
5 Jan.	—	0·47	0·78	3·44	8·75	1·41	5·15	0·47	0·62	—	0·47
13 Jan.	0·14	1·27	1·13	1·83	5·49	0·84	2·54	0·28	0·42	—	0·56
18 Jan.	0·16	0·66	1·83	2·00	5·33	1·33	3·50	0·16	0·83	—	0·50
Means	0·06	1·27	1·02	2·28	9·19	1·18	3·62	0·57	0·48	0·02	0·41

A third fauna may also be taken into consideration, namely that living in the soil immediately adjacent to the leaf bases of the *Bromus*. In Table 7 the means of Tables 5 and 6 are expressed as percentages and compared with the percentage composition of the surface soil fauna. This latter was obtained by washing out a mixed sample of surface soil, totalling approximately 8 cu. in., collected immediately below the grass samples taken on 24 November 1937 and yielding, in all, ninety-four organisms.

Table 7. *Percentage composition of samples from* (*a*) *grass up to* 2 *in. above soil* (*ordinary samples*), (*b*) *leaf bases of grass at soil surface, and* (*c*) *surface soil*

	P. subcrassus	Other Collembola	*H. pallidulus*	*A. aphidioides*	Immature mites	Trombidiformes	Oribatidae	*E. stabularis*	Other mites	Thrips	Other species
(*a*)	0·4	3·9	26·3	6·7	26·8	16·5	4·6	10·2	1·5	2·0	1·1
(*b*)	0·3	6·3	5·0	11·3	45·8	5·9	18·0	2·8	2·4	0·1	2·0
(*c*)	—	54·3	1·1	—	8·5	3·2	18·1	—	2·1	—	12·8

This table indicates that there exists a distinct vertical zonation in the Brometum fauna and that the soil community is essentially distinct from that inhabiting the grass, the chief link being the Oribatid mites which form approxi-

mately 18 % of the soil and leaf base faunas. The 54·3 % of Collembola in the soil comprises chiefly a species which does not occur in the grass, *Tullbergia krausbaueri* Born.

This zonation, at least in the grass fauna, is subject to variation with changing climatic conditions. The relative wetness of all the 1937–8 samples does not permit a direct demonstration of this, but the definite positive correlation of *H. pallidulus* density with water content shows that a downward movement of this species and probably certain others (Section 6) to a lesser extent, does occur. It was demonstrated in 1935–6 (Ford, 1937) that on dry days the upper regions of the grass tussocks (not sampled in the present census) were almost devoid of fauna.

6. MOVEMENT OF SPECIES IN RESPONSE TO WATER

We may obtain more precise information on the movement of species in response to water by calculating the coefficients of correlation (r) between population density of the various species and the water content of the samples (Table 4). The results of these calculations are given in Table 8.

Table 8. *Population density of various species and water content of samples. Values for r and P*

	r	P ($n=50$)	
P. subcrassus	+0·181	>0·10	Not significant
H. pallidulus	+0·448	<0·01	Significant
A. aphidioides	−0·249	0·10–0·05	Doubtful
Immature mites	+0·320	0·05–0·02	Fairly significant
Trombidiformes	−0·005	>0·10	Not significant
Oribatidae	+0·266	0·10–0·05	Doubtful
E. stabularis	+0·315	0·05–0·02	Fairly significant
Whole population	+0·437	<0·01	Significant

It is evident from the above table that the mite *H. pallidulus* is strongly affected by the presence of abundant moisture in the grass and it is this species which contributes chiefly to the positive correlation shown by the whole fauna. This being the case, it would appear that a curve drawn through the outstanding points on the curve given in Fig. 2 (i.e. those obtained from samples with high water content), would approach closer to the true state of affairs than that actually shown.

The second most abundant species, *A. aphidioides*, has a doubtful negative correlation and the value for P indicates that the number of samples taken was insufficient to permit of any certainty with regard to this species. It may be noted here that *A. aphidioides* appears to show a periodic fluctuation in density, with intervals of approximately 3 weeks between each peak, from 19 October till 1 February. This is shown in the unsmoothed curve in Fig. 2 and, more clearly, as a smoothed curve, in Fig. 4. A comparison of this curve with that for water content, in Fig. 2, indicates that it is unlikely that the periodicity in

the *A. aphidioides* fluctuations was directly due to the action of moisture on activity of this species.

The positive correlation shown by the group of immature mites (excluding Trombidiformes) is probably a correct one, but it is not possible to come to any definite conclusion with regard to it, owing to the habit of these forms of aggregating to form localized points of very high density. This habit, as much as the correlation of activity with moisture, must be regarded as being the cause of the irregularity in the curve for immature forms (Fig. 2).

7. Fluctuations in population density

Various points about fluctuations were observed, especially in the predominant species, *H. pallidulus*. Commencing at a very low level in October, this species multiplies rapidly and reaches a peak in the middle of December.

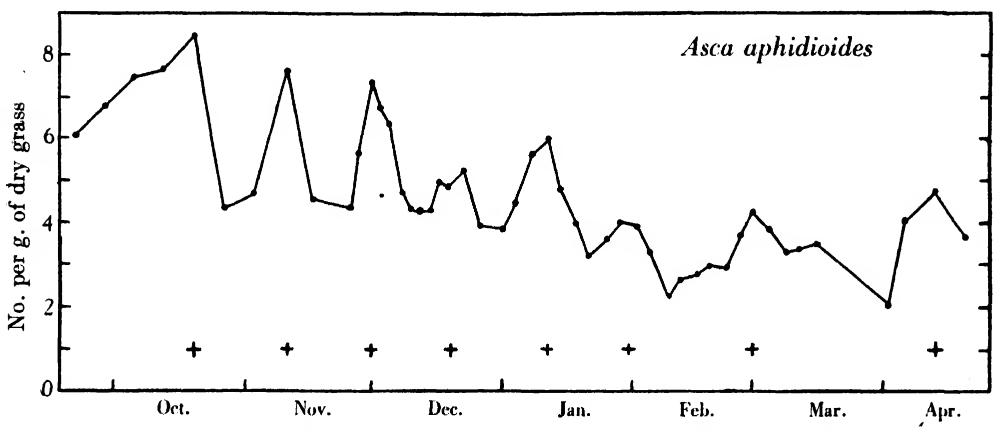

Fig. 4. Population trend of *Asca aphidioides*, 1936–7. (Smoothed curve.)

This occurred in each of the three seasons during which observations were made. In the first, however, of 1935–6, the decline following the December peak was followed by another increase, in which the springtail, *P. subcrassus*, also partook. In regard to the first decline, shown in all three seasons, it would appear that the reversal of the population trend is probably due to biotic causes. Table 9 shows some of the climatic averages during the ascent of the population in November and December and during the decline in January and February.

Table 9. *Climatic averages for November–December and January–February* 1936–7

	November–December	January–February
Maximum temperature	7·9° C.	8·5° C.
Minimum temperature	2·1° C.	2·4° C.
Lowest temperature	−3·8° C.	−3·5° C.
Rainfall (total)	4·657 in.	7·992 in.
Water content of samples	157%	188%
Sunshine hours (total)	111·16 hr.	117·55 hr.

There is evidently no significant difference between the temperatures during the two periods, nor in the amount of sunshine. The only feature in which there is a difference is moisture. Here the January–February period is distinctly wetter, and therefore apparently more favourable to the Acarine population than November and December. It would appear from this table that the general climatic conditions of January and February would tend to favour the increase of the population rather than to cause a decline. A further point in favour of a biotic explanation of the reversal of the population trend in December is the similarity in the densities reached at the peak, and the close approximation of the time at which the peak occurred in the three winters. This applies also to the springtail, *P. subcrassus* which, though not abundant in 1936–7, followed a similar trend (see Section 8).

8. Age distribution of the *Pseudachorutes subcrassus* population

Metamorphosis does not occur in Collembola and the size of individuals increases at successive moults. Although this increase in size is not necessarily even nor the time between moults equal, we may, nevertheless, obtain figures roughly proportional to age by measuring the length of these insects. With some species at any rate, ecdysis and growth does not cease at maturity (Macnamara, 1919).

During the counting of samples, measurements of all individuals of *P. subcrassus* were made by means of a micrometer eyepiece, from 5 October 1936 to 19 April 1937. Although it transpired that this species was only present in small numbers, a definite increase in population density, culminating in a peak at the beginning of January, was detectable. This is shown as a smoothed curve, derived from the data of Table 4, in Fig. 5. The same figure also shows a similarly smoothed curve for the change in average length of individuals comprising the population (Table 10). The length of these insects varied between 0·20 and 0·75 mm., the mean of 850 measurements being 0·425 mm. By selecting an arbitrary value, in this case 0·40 mm., we may calculate the percentage of the population, at each date, of length greater than this. The smoothed curve so obtained, follows, as might be expected, approximately the same trend as that for the average length. The technique used in sampling is not efficient for procuring the youngest individuals, which are unable to resist the drying process used in extraction. The average length therefore is somewhat less, in reality, than that given above. Similarly, in the consideration of the length (age) classes in the next paragraph, the youngest class, during the period of increase, should have a much greater extension.

There is not sufficient data to enable us to make an accurate division into age classes of the population at each sampling date, but we may summate the age classes in each month. The result of this is shown in Table 11.

Since the sampling methods that were used failed to include the youngest individuals, we may therefore regard the figures of the first column of Table 11 as

Table 10. *Mean length changes in* P. subcrassus *population*

Date	Number measured	Mean length	% over 0·4 mm.	Date	Number measured	Mean length	% over 0·4 mm.
5 Oct.	10	0·49	80·0	11 Jan.	33	0·49	75·7
12 Oct.	7	0·45	71·5	14 Jan.	34	0·46	70·5
19 Oct.	16	0·38	43·8	18 Jan.	30	0·44	56·6
26 Oct.	8	0·34	25·0	21 Jan.	20	0·40	40·0
2 Nov.	30	0·39	43·4	25 Jan.	36	0·48	77·8
9 Nov.	10	0·33	20·0	28 Jan.	22	0·48	63·6
16 Nov.	26	0·37	30·8	1 Feb.	10	0·49	90·0
23 Nov.	16	0·35	31·3	4 Feb.	24	0·43	58·4
25 Nov.	16	0·37	37·5	8 Feb.	13	0·49	84·7
27 Nov.	22	0·37	27·3	11 Feb.	11	0·39	45·5
30 Nov.	40	0·40	45·0	15 Feb.	23	0·49	78·2
2 Dec.	20	0·45	60·0	18 Feb.	10	0·44	50·0
4 Dec.	17	0·35	35·3	23 Feb.	6	0·43	83·4
7 Dec.	48	0·40	41·7	25 Feb.	6	0·45	66·6
9 Dec.	29	0·37	31·0	1 Mar.	10	0·49	80·0
11 Dec.	20	0·43	55·0	4 Mar.	4	0·56	100·0
14 Dec.	21	0·38	33·3	8 Mar.	9	0·49	100·0
16 Dec.	38	0·40	39·5	11 Mar.	8	0·37	37·5
18 Dec.	36	0·38	38·9	15 Mar.	4	0·49	100·0
21 Dec.	23	0·42	43·5	18 Mar.	12	0·40	58·4
28 Dec.	22	0·42	54·5	1 Apr.	4	0·32	0·0
31 Dec.	32	0·39	37·5	5 Apr.	9	0·49	77·8
4 Jan.	56	0·42	48·2	12 Apr.	3	0·34	33·3
7 Jan.	43	0·50	74·4	19 Apr.	3	0·54	100·0

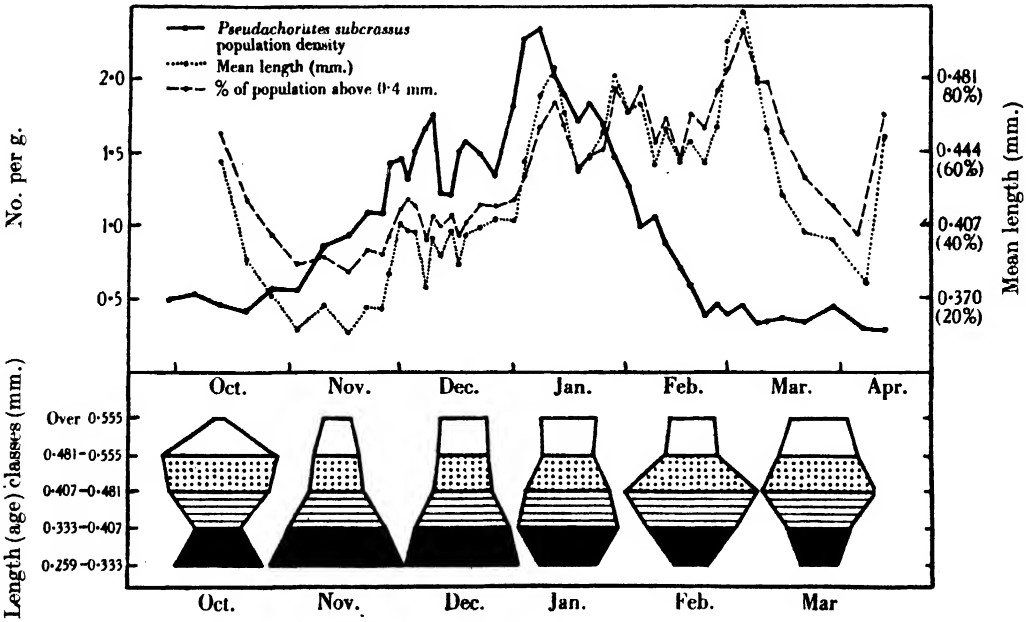

Fig. 5. *Pseudachorutes subcrassus.* Population trend and age distribution.

incomplete. The length (age) distribution diagrams of Fig. 5 are based on the figures from Table 12, in which the data of Table 11 are arranged on a percentage basis after the exclusion of the lowest class, below 0·259 mm.

These results provide a striking confirmation of the existence of a true increase and decline in the population of *P. subcrassus*, in spite of its low

Table 11. *Length (age) classes of* P. subcrassus *each month, October* 1936 *to March* 1937

	Below 0·259 mm.	0·259–0·333	0·333–0·407	0·407–0·481	0·481–0·555	Above 0·555 mm.
Oct.	8	8	4	9	10	1
Nov.	24	51	37	20	17	11
Dec.	36	86	69	43	37	34
Jan.	1	38	65	55	35	36
Feb.	2	10	25	37	15	13
Mar.	3	5	8	14	10	7

Table 12. *Percentage length (age) composition of* P. subcrassus *population*

	0·259–0·333	0·333–0·407	0·407–0·481	0·481–0·555	Above 0·555 mm.
Oct.	25·0	12·5	28·1	31·2	3·1
Nov.	37·5	27·2	14·7	12·5	8·1
Dec.	32·0	25·7	16·0	13·8	12·6
Jan.	16·6	28·4	24·0	15·3	15·7
Feb.	10·0	25·0	37·0	15·0	13·0
Mar.	11·4	18·2	31·8	22·7	15·9

density, for they are precisely what would be expected in such a case. Hitherto age distribution in populations has only received detailed attention in human communities and it is of interest to find that the undercutting of the age pyramid, by the decline in natality during the fall of the population in January and February, finds a parallel in the similar undercutting now taking place in many European countries, which, it is believed, is initiating a decline in the human population. (See, for example, Carr-Saunders, 1936).

Little work has been done on the development of Collembola, save for *Sminthurus viridis* L., a species active during summer, not saprophagous and therefore with little bearing on the present study. However, MacLagan (1932) records for it a life-cycle lasting approximately 50 days, with seven instars, sexual maturity being reached before the completion of the last instar, at about 40 days. Each female may lay up to 100 eggs. *S. viridis* is a much larger animal than *P. subcrassus* and possibly may take longer to reach maturity, but reproduction rates similar to those of *S. viridis* would be sufficient to account for even larger increases in population than were observed for *P. subcrassus* in 1935–6.

9. Distribution of the brometum fauna

It has been mentioned that in 1936–7 samples were grouped in such a way that means for population densities within individual *Bromus* tussocks could be obtained. Three such means were obtained on each sampling date and by use of the standard deviation (σ) formula measures of the variability between tussock means were calculated. Table 13 gives the mean total population densities, of all species (m), with the standard deviation and coefficient of variability $\left(\frac{\sigma 100}{m}\right)$ between tussock means. The data of this table are plotted as

smoothed curves $\left(\frac{a+b+c}{3}, \frac{b+c+d}{3}\right)$ in Fig. 6. Roughly, these curves show that at the beginning of the season, with a low population density, the variability is high; with an increase in the population, the variability decreases simultaneously; at the end of the season, when the population density is again low, the variability once more increases.

Table 13. *Mean total population densities* (m), 1936–7, *with standard deviations* (σ) *and coefficients of variability* $\left(\frac{\sigma 100}{m}\right)$.

Date	Total population (m)	σ	$\frac{\sigma 100}{m}$	Date	Total population (m)	σ	$\frac{\sigma 100}{m}$
21 Sept.	16·42	2·66	16·1	7 Jan.	29·14	7·98	27·4
28 Sept.	19·84	10·71	54·0	11 Jan.	28·16	4·92	17·5
5 Oct.	18·58	7·46	40·1	14 Jan.	26·70	3·56	13·2
12 Oct.	18·35	12·20	66·4	18 Jan.	45·29	13·09	28·9
19 Oct.	16·64	9·42	56·5	21 Jan.	28·11	6·03	21·4
26 Oct.	17·39	5·54	31·8	25 Jan.	25·95	1·37	4·6
2 Nov.	30·17	19·73	64·8	28 Jan.	22·11	3·35	15·1
9 Nov.	19·30	7·13	37·0	1 Feb.	21·33	2·86	13·4
16 Nov.	23·52	9·27	39·4	4 Feb.	21·20	1·95	9·2
23 Nov.	14·21	6·37	44·7	8 Feb.	29·34	9·53	32·4
25 Nov.	34·20	7·95	23·2	11 Feb.	16·03	4·18	27·3
27 Nov.	30·33	0·59	1·9	15 Feb.	22·30	7·67	34·3
30 Nov.	39·54	10·81	27·3	18 Feb.	21·63	2·93	13·5
2 Dec.	39·93	8·93	22·4	23 Feb.	16·83	4·08	24·3
4 Dec.	23·60	7·96	33·7	25 Feb.	21·46	10·14	47·2
7 Dec.	27·03	9·53	35·2	1 Mar.	18·03	8·91	49·4
9 Dec.	26·94	4·85	18·0	4 Mar.	15·37	5·41	35·2
11 Dec.	45·79	8·01	17·5	8 Mar.	22·85	10·76	47·0
14 Dec.	38·26	13·22	34·5	11 Mar.	24·67	16·91	68·4
16 Dec.	34·84	19·81	56·7	15 Mar.	14·83	4·04	27·2
18 Dec.	33·96	15·62	45·9	18 Mar.	16·19	3·60	22·4
21 Dec.	26·22	5·88	22·4	1 Apr.	8·20	2·33	28·3
28 Dec.	30·08	4·76	15·8	5 Apr.	16·57	8·46	56·8
31 Dec.	25·18	7·45	29·5	12 Apr.	11·69	2·24	18·5
4 Jan.	28·35	2·62	9·2	19 Apr.	21·39	9·57	44·6

The following explanation is offered for these observations. It seems evident that the increase of the fauna in October is initiated by a falling temperature and, more especially, by the increase of the moisture in the habitat. (Thompson, 1924, found that the soil population commenced to increase earlier after a very wet summer and autumn.) It is reasonable to suppose that some tussocks, by their density of growth, etc., afford, in unfavourable conditions, better shelter than others for their fauna. These tussocks, therefore, under such conditions, will tend to support a higher population than those not so suitable. This would account for the high variability shown when the population is at a low level. With the amelioration of conditions brought about by approach of winter, more and more tussocks become capable of supporting higher populations and thus there is a decrease in variability between tussock populations and an increase in the total population. When the population again decreases,

variability once more increases, since the population would tend to survive longest in the most favourable tussocks.

That the high variability at the beginning and end of the season is due to the differences between individual tussocks is supported by the increase in-

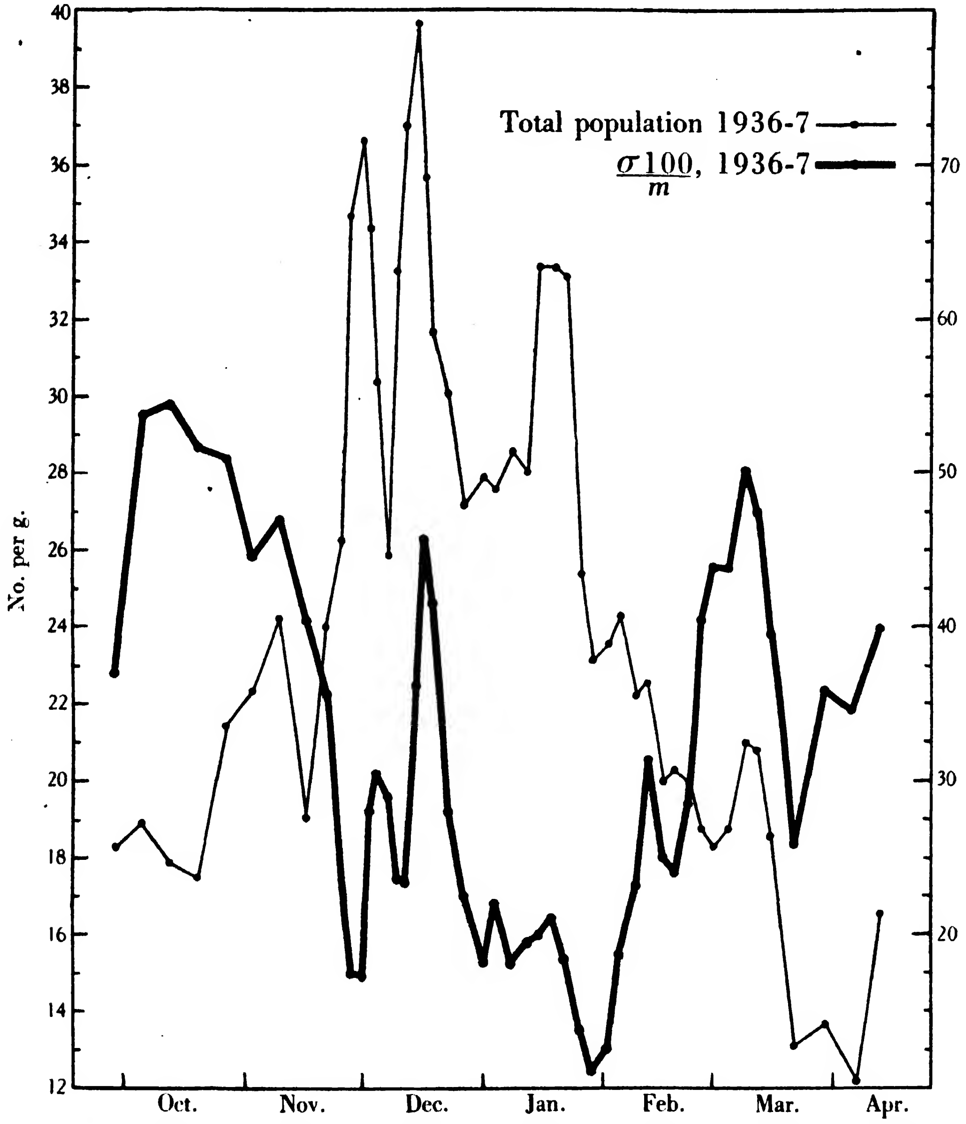

Fig. 6. Smoothed curves for total population and coefficients of variability, 1936–7.

variability occurring in December immediately following, but not coincident with, the peak of 15 December. It has already been shown that the sharp decline following this peak, from 4 to 28 December is not a true one, but is due to a response by *H. pallidulus*, to drought. We may, therefore, attribute this brief period of high variability to the same cause acting with greater or lesser force in unfavourable and favourable tussocks.

10. Discussion

Before reviewing the results of this community census it is appropriate to discuss briefly the object of community analysis in general, and its relationship to other biological studies. It is generally agreed that the aggregate of organisms of all kinds inhabiting any naturally limited area interact among themselves and with the environment and, in so doing, form a system more or less stable or continuously approaching stability. According to some theories (e.g. Phillips, 1931, 1935) this system is, in fact, an organism: a claim based chiefly on analogies with organisms as commonly understood. It appears preferable, as yet, to refer to organic communities as *ecosystems* (Tansley, 1935) since the nature of the organization characteristic of them has not been critically discussed. The organization of organisms (in the strict sense) has, however, received considerable attention, particularly from Woodger (1929), and, since the kind of organization described by him has great pragmatic value in explaining the status of community studies, it will receive some comment here.

According to Woodger's classification the parts of which an organism is formed stand in a hierarchical relation to one another: the whole organism—organ systems—organs—cells—parts of cells, etc., etc. (This is a simplified version of Woodger's scheme, p. 309, to which it is not possible to do justice in a short space.) The components and the relationships of components in any level of the hierarchy "explain" the entities which form the level above. The whole organism can be "explained" in terms of the nature and relationships of organ systems, these in turn by the nature and relationships of organs, and so on. It is shown that "an entity having the hierarchical type of organization such as we find in the organism requires investigation at all levels and investigation of one level cannot replace the necessity for investigation higher up in the hierarchy" (p. 309). A similar view is expressed by Needham (1936) who states of Wilhelm Roux that "the course he set...involved the analysis of development, not into simple physico-chemical processes directly, but into more complex organic processes. He showed that it was possible, and indeed necessary, to deal first with large packets of factors in the biological organism, before proceeding to the finer analysis of the smaller packets."

The application of these notions to community analyses is not difficult to perceive. One way of analysing an ecosystem is to list all the species and, by studying each individually, to discover their various activities and so build up a picture of the community as a food chain. But this method fails to discover many important phenomena characteristic of communities. It is, in fact, studying one level in the hierarchy while ignoring higher levels. The study of the habits of individuals fails to yield any information on the phenomena produced by population interactions, unless these have been the object of previous study. As an illustration we may take a very simple ecosystem, for example, one in which two species of Protozoa, A and B, of which A preys upon B, exist

together with a bacterium, C, which forms the food of B, the physical environment remaining constant. Now if we proceed to investigate the habits of these three species we shall arrive at the food chain $C \rightarrow B \rightarrow A$. Further than this it will not be possible to get.

A much more useful method will be to study first the behaviour of the populations of these species. It will not be necessary to have any previous knowledge of their habits. We may then disover that the populations fluctuate rhythmically and that these fluctuations bear definite quantitative relationships to one another and to the densities of population. We may then proceed to apply the methods used in the first study, and the food chain now discovered explains the fluctuations and a far more complete idea of the working of the community is obtained than could possibly have been arrived at by only studying the habits of the individuals comprising it.

The analysis of the ecosystem in terms of behaviour of individuals, that is, the construction of a food chain, and the correlation of physiological requirements with the physical environment, take no account of a factor of the first importance in descriptions of community behaviour, namely, time. Omission of the time factor in community studies results in a failure to disclose the dynamic nature of the equilibria characteristic of ecosystems and data so obtained are of very limited value.

It is in the belief that in analysis of ecosystems descriptions of population behaviour must precede the study of the physiological requirements of individual species that the present investigation has been made. It is an attempt to describe a small section of a much larger ecosystem, during a small part of its existence, in terms of population change. Previous analyses have shown (Ford, 1937) a similarity of behaviour in ecosystems in which the predominating animals are Acarina and Collembola. This is to be expected since related organisms, having similar physiological requirements, will tend to produce similarities in the phenomena exhibited by the communities they form. Collembola-Acarina ecosystems occur, in temperate regions generally, wherever there is abundance of decaying vegetation and moisture. The period of greatest activity is, in Europe, in winter, during cold wet weather.

The present study endeavours to describe quantitatively the behaviour of a Collembola-Acarina-*Bromus* ecosystem during its period of greatest activity. It has attempted to show approximately the densities of population of its component species at the commencement of winter activity, the time taken in reaching a maximum density and the course of the declining population. In addition to this description of the changes within the ecosystem during the passage of time, the census has permitted a preliminary analysis to be made of the spatial distribution of the various species and the changes in distribution taking place during climatic variation and during alterations in population density. It is not claimed for the data given that they represent more than a rough approximation to reality, but it is believed that the results are suffi-

ciently consistent to allow the major features of this ecosystem, during the time it has been under observation, to be outlined. It is not, of course, to be supposed that the details of the census will be repeated in another season, indeed, this is evident from a comparison of some features of the Brometum populations in the three seasons with which we have been concerned.

11. Summary

1. This paper concludes three series of censuses of a Collembola-Acarina (springtail-mite) community inhabiting tussocks of the grass *Bromus erectus*.

2. Changes in the composition of the fauna of the Brometum during the winters of 1935–6, 1936–7, 1937–8 are reviewed. The principal change was the decline between the first and second winters of the springtail, *Pseudachorutes subcrassus*. This may have been the cause of an increase, subsequently, in the population density of the remaining species.

3. Sampling at different levels revealed a distinct vertical zonation in the grass fauna which is subject to alterations during changes in the moisture content of the habitat. The soil fauna is distinct from that of the grass.

4. A marked positive correlation between the density of the mite *H. pallidulus* with the water content of samples indicates that this species descends to the bases of the grass leaves during relatively dry periods. There is no correlation in the case of *P. subcrassus* nor with Trombidiform mites. *A. aphidioides* has a doubtful negative correlation. This latter species though abundant in 1936–7 showed a declining population with a periodic fluctuation at intervals of approximately 3 weeks throughout that winter. This periodicity was apparently independent of moisture variation, as of other measured climatic factors.

5. Population increase commenced in October, reaching a peak in the middle of December, in each winter. In 1936–7 the decline from this peak was continuous, thus differing from 1935–6 when another increase took place at the end of January. It would appear that the decline following the December peak is independent of changes in the physical environment, though further work on different lines would be needed to investigate a biotic cause, if any.

6. The approximate age distribution of *P. subcrassus* was analysed and shown to correspond, in its changes during the fluctuation, to that expected in a growing and declining population.

7. The distribution of the fauna, expressed in terms of the standard deviation, showed that at the commencement of the population increase variability is high. Variability decreases as the increase in population continues, but increases again with the ultimate decline of the population.

8. A discussion is devoted to the purpose and status of ecosystem analyses.

REFERENCES

Carr-Saunders, A. M. (1936). "World population. Past growth and present trends." Oxford.

Ford, J. (1937). "Fluctuations in natural populations of Collembola and Acarina." J. Anim. Ecol. 6: 98–111.

MacLagan, D. S. (1932). "An ecological study of the 'lucerne flea' (*Smynthurus viridis*, Linn.). I." Bull. Ent. Res. 23: 101–45.

MacNamara, C. (1919). "Remarks on Collembola." Canad. Ent. 51: 73–80, 265–71.

Needham, J. (1936). "Order and life." Cambridge.

Phillips, J. (1931). "The biotic community." J. Ecol. 19: 1–24.

Phillips, J. (1935). "Succession, development, the climax, and the complex organism: an analysis of concepts. Part 3. The complex organism: conclusions." J. Ecol. 23: 488–508.

Tansley, A. G. (1935). "The use and abuse of vegetational concepts and terms." Ecology, 16: 284–307.

Thompson, M. (1924). "The soil population. An investigation of the biology of the soil in certain districts of Aberystwyth." Ann. Appl. Biol. 11: 349–94.

Woodger, J. H. (1929). "Biological principles. A critical study." London.

POPULATIONS, TERRITORIES AND BIOMASSES OF ANTS AT THORNHILL, YORKSHIRE, IN 1937

By WALTER PICKLES

(*With* 1 *Figure in the Text*)

1. Introduction: changes in nest populations

In the summer of 1937 the survey of ants' nests at Thornhill was repeated. No new species of ants were found, and many of the old nest mounds had become re-inhabited, i.e. nos. 1, 2, 3, 6, 8 A, 20 and 21. Of these nests, nos. 1 and 3 were *Acanthomyops* (*Chthonolasius*) *flavus* F.; nos. 6, 8 A and 21 were *Myrmica ruginodis* Nyl.; and nos. 2 and 20 were *Formica fusca* L. Nest 21 was a mixed nest of *A. flavus* and *M. ruginodis*. In 1936 only *M. ruginodis* was present, so that the former species must have migrated to the spot. Nest 6, although inhabited again, did not contain the same species as in 1936. Previously *F. fusca* inhabited this nest, but in 1937 *M. ruginodis* occupied it; and even then only as a temporary nest.

In 1936 I marked 50 inhabitants of nests 1, 8 A and 15 (a nest of each species) but have been unable to find any of these marked ants, this may possibly have been due to the fact that the mutilated ants were killed or died naturally, or that the whole colony has moved out of my area of census. Nest 15 was not inhabited at all this year (1937); but nests 1 and 8 A have been inhabited by the same species again though the populations have decreased in both cases: from 1543 to 152 in the case of nest 1 and from 343 to 187 in the case of nest 8 A. If these are members of the 1936 nests, which is by no means certain, then it is quite possible for all the mutilated ants to have succumbed in some way mentioned above.

In the cases of *Myrmica ruginodis* and *Formica fusca* it seems quite likely, from the way stones are inhabited at one time and not at another, that they are generally on the move, staying a few weeks under one stone, and moving on to another, particularly if disturbed.

With regard to *Acanthomyops flavus*, although they are not so active in foraging over the surface of the ground as the other two species, they move from place to place: hence the appearance of this species under the stone of nest 21 in 1937.

2. Discussion of the species

(*a*) *Acanthomyops flavus*

In previous years this species was not noticed to be abroad foraging and it was stated that I had never seen them leave the nest mound (**4**, **5**). Early in the summer months several small colonies of these ants, of say two dozen to thirty or so in number were discovered. I thought, at first, that possibly

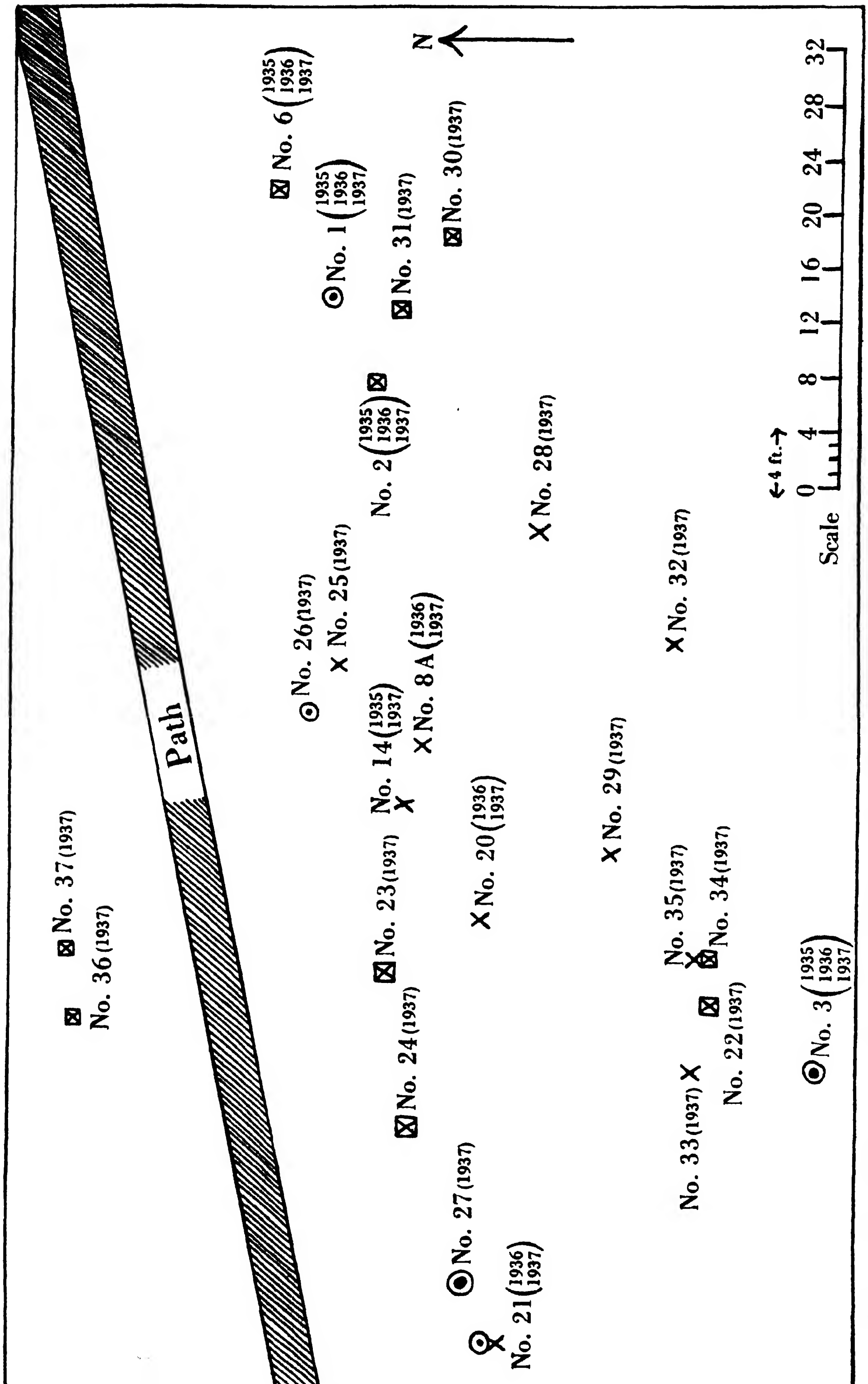

Fig. 1. Plan of nests on the area under observation during 1937. The dates of the nests are in brackets. × nests of *Myrmica ruginodis*; ⊠ nests of *Formica fusca*; ⊙ nests of *Acanthomyops flavus*; mixed nest of *M. ruginodis* and *A. flavus*.

having disturbed nests 1 and 3 in the past two summers, the effect had been to distribute many of the inhabitants over the area. However, I found that Carey & Diver (**1**) had found a similar state of affairs at South Haven Peninsula, Dorset. This distribution then was not entirely artificial and I began to dig round the nests to discover whether there was any way of accounting for this distribution. At a spot 8 ft. from nest no. 27 was found a small colony of about a dozen *Acanthomyops flavus* together with about an equal number of *Myrmica ruginodis.* They were on the roots of grass and were attending to some aphides (*Tetraneura ulmifoliae* Baker). I have since discovered specimens of these aphides on the roots of grass in different parts of the area. These aphides may possibly help in the distribution of the species as Theobald (**2**) mentions that the apterous viviparous females are found in ants' nests, e.g. *Lasius* (*Acanthomyops*) *flavus* and *Myrmica ruginodis.*

The aphides, *Tetraneura ulmifoliae,* were found on the roots of the grass, *Holcus mollis,* which grows fairly generally among the bracken and also on nest 27. On other parts of the hillside there are nest mounds completely covered with this grass. Nests 1, 3, 21 and 27 also, are covered with the grass *Deschampsia flexuosa.* The greater number of these nests on the whole hillside are also grass-grown. Possibly there may be some connexion between the long underground roots of *Holcus mollis* with their accompanying aphides and the underground feeding territory of *Acanthomyops flavus.*

With regard to the population figures of this species (see Table 2), the decrease in population of nests 1 and 3 may be largely artificial, due to them having been disturbed in two previous summers. The upheaval has probably caused them either to die off or move to another part of the area. This may be one reason for the great decrease in numbers of no. 1 compared with 1936, as near the stone under which they have lived in 1937 on the mound, there was a heap of dismembered ants. Among this heap were the abdomens, thoraxes and heads of a number of females, which clearly shows that, after the nest had been returned last summer, there was a considerable mortality among the inmates of this nest.

I have mentioned earlier that the ants are constantly moving about from stone to stone. There was one very interesting example of this in connexion with nest no. 27. A flat stone was here used as a nursery. At one period in May and June there were many cocoons beneath this stone. Later in the summer, on 25 August and until 18 September it was out of use. From the latter date until 2 October it has been used as a nursery by *Formica fusca, Acanthomyops flavus* still occupying the surrounding ground.

There were altogether 5 nests of *A. flavus,* of which nos. 1, 3, 21 (mixed *Myrmica ruginodis-Acanthomyops flavus*) and 27 were permanent ones and no. 26 was a temporary nest, lasting from 20 May 1937 to 11 August 1937. As a result of digging up the ground round about this nest, several aphides (*Tetraneura ulmifoliae*) were found on the roots of the grass.

(*b*) *Formica fusca*

Of this species of ant, altogether 10 nests occurred, 6 being temporary and 4 lasting throughout the whole summer. The stones of nests 2 and 6 have been occupied during the past three summers; but it is fairly certain that the occupation has not been continuous and by the same ant colonies. Nest no. 2 became deserted altogether and no. 6, which was originally a nest of *F. fusca* (lasting until 6 August 1937), became inhabited by *M. ruginodis* as from that date until previous to 11 August.

There have been cases of temporary sharing of the stone of one species by another. For instance on 4 August 1937 I found the stone of nest 8 A (*M. ruginodis*) being used as a nursery by *F. fusca* (workers and cocoons being under the stone). Two days later when the nest was dug up for counting, they had vanished.

(*c*) *Myrmica ruginodis*

There have been altogether 10 nests of this species of ant, 4 being temporary and 6 being permanent ones. Owing to the very short existence of nest 6 as a *M. ruginodis* nest, from 6 August until sometime previous to 11 August when I paid my next visit, and found it had vanished, it can hardly be called a temporary nest; but rather it seems to have been a "rest" by a nest of ants on the move to new quarters. As mentioned earlier, nest 21 has been a mixed one of *M. ruginodis-A. flavus*.

From this discussion of the species we see that in the case of *A. flavus*, there have been 3 more nests than in 1936, although the 1936 old nests have also been occupied again. In the case of *F. fusca*, there have been fewer permanent nests than there were in 1936, 4 as against 5 in 1936. There have been 10 nests altogether this year, while the total number of nests of this species in 1936 was 7, an increase of 3 nests.

With regard to *M. ruginodis* there have been 10 nests as against 7 last year.

The total number of nests this year has been 25 (reckoning the mixed nest no. 21 as two) as against 16 last year (again counting nest no. 2 of 1936 as two). From this we should expect that there would be an increased population this year, but as the number of permanent nests has been the same as last year (1936) the total population has been roughly the same, being 8246 in 1936 and 8572 in 1937, thus showing a slight increase on 1936.

3. METHODS

Population determinations. As in my previous surveys on ant populations (**3**, **4**, **5**) the ants' nests were dug up and the living inhabitants counted as described previously.

Weights. The same method was used as in 1936 (**5**) for the weight determinations of the nests.

4. Territories

During this survey I have not observed any ant to travel more than the maximum distances recorded in previous years, namely 26 ft. for *Formica fusca* and 10·25 ft. for *Myrmica ruginodis*. This gives a territory of 2124 sq. ft. for *F. fusca* and 330·18 sq. ft. for *M. ruginodis*.

With regard to *Acanthomyops flavus*, arising out of my observations this year, some modification of statements made in my previous records on surveys made in 1935 and 1936 (**4**, **5**) is necessary. In these surveys I stated that *A. flavus* had no feeding territory; but owing to the fact that it has been found attending to the aphid *Tetraneura ulmifoliae* at varying distances away from the nests, then it must have some feeding territory.

I have found isolated groups of *A. flavus* attending these aphides at a distance of 8 ft. from nest 27 under a stone. There were also in this case a number (roughly a dozen or so) of *M. ruginodis* under the same small stone, and crawling about the roots of the grass *Holcus mollis* on which the aphides were situated. Several aphides were picked up by the *M. ruginodis* and carried about, and I observed a specimen of *A. flavus* to pick up an aphid and carry it down a hole. On another occasion a solitary specimen of *A. flavus* was found under a small stone at a distance of 3 ft. from nest 1. Digging around disclosed no other ants about.

Under these circumstances I hesitate to give a definite figure for the feeding territory of this species; but that it has a feeding territory seems certain now.

5. Populations of the nests

The censuses were made by digging up the nests and counting the living inhabitants; males, females, workers and immature forms being counted separately. After being counted the ants were returned to the same spot.

Table 1. *Analysis of populations of nests*

Name of species	Date	No. of nest	Workers ☿	Males ♂	Females ♀	Larvae	Naked pupae	Cocoons ☿	Female cocoons	Total
Acanthomyops flavus	10 July 1937	3	1333	2	1	16	—	124	5	**1481**
	11 Aug. 1937	21*	1763	25	3	—	—	78	—	**1869**
	25 Aug. 1937	1	152	—	—	—	—	—	—	**152**
	8 Sept. 1937	27	1127	—	1	—	—	—	—	**1128**
Formica fusca	4 Aug. 1937	30	326	—	1	43	127	112	—	**609**
	27 Aug. 1937	31	333	—	1	—	—	8	—	**342**
	25 Sept. 1937	36	603	—	4	—	—	31	—	**638**
	2 Oct. 1937	37	189	—	—	—	—	—	—	**189**
Myrmica ruginodis	19 July 1937	29	93	—	—	14	5	—	—	**112**
	6 Aug. 1937	8A	185	—	2	—	—	—	—	**187**
	11 Aug. 1937	21*	28	24	—	—	—	—	—	**52**
	11 Sept. 1937	32	456	—	1	—	—	—	—	**457**
	18 Sept. 1937	33	878	—	1	20	—	—	—	**899**
	25 Sept. 1937	35	457	—	—	—	—	—	—	**457**

* Mixed nest of *Myrmica ruginodis-Acanthomyops flavus.*

An analysis of the populations of each nest is shown in Table 1. From this it will be seen that as in previous years the nests of *Acanthomyops flavus* (except nest 1) are the most populous, whilst, on the average, the nests of *Formica fusca* are more populous than those of *Myrmica ruginodis*.

Table 2

Name of species	No. of nest	Population in 1935	Population in 1936	Population in 1937
Acanthomyops flavus	1	5,743	1,543	152
	3	5,613	2,210	1,481
	*21	—	—	1,869
	27	—	—	1,128
	Total	11,356	3,753	4,630
Formica fusca	6	275	720	—
	12	73	—	—
	9	218	—	—
	11	65	—	—
	13	143	352	—
	17	—	766	—
	19	—	13	—
	†2	249	482	—
	15	—	56	—
	30	—	—	609
	31	—	—	342
	36	—	—	638
	37	—	—	189
	Total	1,023	2,389	1,778
Myrmica ruginodis	†2	279	78	—
	10	1,534	—	—
	14	233	—	—
	8	660	(8A) 343	(8A) 187
	5	—	1,159	—
	18	—	489	—
	*21	—	35	52
	29	—	—	112
	32	—	—	457
	33	—	—	899
	35	—	—	457
	Total	2,706	2,104	2,164

* Mixed *Myrmica ruginodis-Acanthomyops flavus* nest.
† Mixed *Formica fusca-Myrmica ruginodis* nest.

In Table 2 a comparison of the populations of the nests in the three years 1935–7 is shown. From this table we see that the population of *Acanthomyops flavus* has increased by 877 on the 1936 census. *Formica fusca* shows a decreased population of 611 on 1936, though, on the average, the nests have been more populous. In the case of *Myrmica ruginodis* the population has remained approximately the same with a slight increase of about 60, though the average population per nest has decreased from 420 to 360. In the three years during which censuses have been taken, the *Myrmica ruginodis* population has fluctuated least of all three species.

Again I found that the stone covering a nest or the mound of one only gives an approximate idea of the size of the population in it (Elton (**6**), Pickles (**3**, **4**, **5**)).

6. Density of population

The density of population may be expressed in three ways: (*a*) the *Economic Density*, i.e. the total population divided by the territory; (*b*) the *Lowest Density*, i.e. the total population divided by the area of the census; and (*c*) the *Greatest Density*. The greatest density is taken as the population of the nests at night. As the nests were dug up either in the early morning or evening, the total populations given may be counted as the greatest densities.

Owing to the fact that at least a definite illustration of the existence of territory among *Acanthomyops flavus* has been given, a provisional "territory per nest" and economic density will be given in Table 3. A definite figure, however, can be given for the lowest density. For density purposes nests 36 and 37 were practically on the verge of the area, and therefore only half of the territory of each nest actually came within the survey. The total territory of these two nests will, therefore, count as one for that species.

Table 3. *Densities of population*, 1937

Name of species	Total population*	Territory per nest	Economic density = Total population / Total territory	Lowest density = Total population / Area of census†
Acanthomyops flavus	4423	3·14 sq. yd.	352·149 per sq. yd.	4·204 per sq. yd.
Formica fusca	1500	236·00 sq. yd.	2·118 per sq. yd.	1·425 per sq. yd.
Myrmica ruginodis	2159	36·70 sq. yd.	9·804 per sq. yd.	2·052 per sq. yd.

* Pupae are not included in this number. † The area of the census is 1052 sq. yd.

From Table 3 it is seen that *Acanthomyops flavus* has the highest economic density and *Formica fusca* has the least.

The species having the greatest lowest density is *A. flavus*, with *M. ruginodis* second, and *Formica fusca* least. The lowest densities of both *F. fusca* and *M. ruginodis* are approximately the same as they were in 1936, namely 1·425 (1937) and 1·471 (1936) for *F. fusca* and 2·052 (1937) and 1·859 (1936) for *M. ruginodis*.

7. Weights of the populations

After each nest had been counted, the inhabitants were weighed and an analysis of these weights is given in Table 4. According to Gause (7) the biological success or failure of a species can be shown by the weights of the living creatures.

In the case of the three species under observation, the total weights of all the living ants were:

Acanthomyops flavus = 2·859 g. (7·037 g. in 1936)
Formica fusca = 5·388 g. (9·616 g. „ „)
Myrmica ruginodis = 4·438 g. (3·665 g. „ „)

These figures show that, as in 1936, *F. fusca* has the greatest weight, though this, like the population, has fallen from its value of the previous season.

Table 4. *Analysis of the weights of the nests (in g.)*

Name of species	No. of nest	Workers ☿	Males ♂	Females ♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	Total
Acanthomyops flavus	3	0·926	0·001	0·010	0·009	—	0·187	0·057	1·190
	21*	1·040	0·012	0·034	—	—	0·030	—	1·116
	1	0·087	—	—	—	—	—	—	0·087
	27	0·453	—	0·013	—	—	—	—	0·466
Formica fusca	30	0·851	—	0·024	0·094	0·321	0·311	—	1·601
	31	0·997	—	0·010	—	—	0·017	—	1·024
	36	2·163	—	0·095	—	—	0·163	—	2·421
	37	0·342	—	—	—	—	—	—	0·342
Myrmica ruginodis	29	0·195	—	—	0·290	0·110	—	—	0·595
	8 A	0·299	—	0·004	—	—	—	—	0·303
	21*	0·041	0·026	—	—	—	—	—	0·067
	32	0·812	—	0·002	—	—	—	—	0·814
	33	1·768	—	0·003	0·004	—	—	—	1·775
	35	0·884	—	—	—	—	—	—	0·884

In the case of *A. flavus*, although the population has increased by nearly 900 on that of 1936 the weight has decreased greatly. This is due to the fact that fewer females and female cocoons have been found in the nests dug up for counting.

M. ruginodis shows an increased weight over the previous season, although the population has remained roughly the same. This is, no doubt, due to fewer larvae being found and more adults being present, 4 out of the 6 nests having no immature forms.

8. The biomasses of the species

The success or failure of the species can be also expressed as the biomass, i.e. the total weight of material per unit area.

Table 5. *Biomasses*

Name of species	Total wt. in g.	Area of census in sq. m.	Wt. per sq. m. in g.
Acanthomyops flavus	2·859	880·51	0·003
Formica fusca	5·388	880·51	0·006
Myrmica ruginodis	4·438	880·51	0·005

F. fusca has the greatest biomass and *A. flavus* the least. The biomass of *M. ruginodis* has increased from what it was in 1936 (i.e. 0·004) and *F. fusca* has decreased from 0·011 to 0·006 g. per sq. m. From this fact and also that the number of nests of *M. ruginodis* has increased, it seems very likely that this species is on the increase in this particular area.

9. Relations with other nests

Often when the stones were lifted up to observe the nests, specimens of the Thysanuran, *Campodia staphylinus*, were crawling about on the under side of the stone and among the ants. This has occurred with all three species of ants. The ants appeared to take no notice of them—they crawled about and eventually disappeared down holes in the soil. Donisthorpe (8) says there are no

myrmecophilus species of Thysanura in Britain. I therefore conclude that the *Campodia* were there purely by accident, as when they were more numerous under a stone covering a nest, they were also plentiful under stones on the rest of the area which were not occupied by ants. The fact that they crawled about amongst the ants when the stone was lifted may be due to the movement throwing them down. In any case I did not observe any of these insects to be attacked by ants; but rather the latter seemed totally indifferent to their presence.

In the layer of decayed bracken leaves and amongst the lower parts of the tufts of grass there were numerous specimens of the Collembolan, *Entomobrya multifasciata*.

10. Conclusions

From this survey, several points of interest have arisen. First, owing to the fact that on several occasions both *Myrmica ruginodis* and *Acanthomyops flavus* have been found attending the same species of aphid (*Tetraneura ulmifoliae*) there may be to some degree a struggle for existence between these two species in the area. If one species of ant is acted upon it should, therefore, produce an effect on the other. This has occurred to some degree.

By the repeated digging up of the nests of *A. flavus*, the population has substantially decreased from what it was in 1935 when it then represented things as they were before any disturbances of an unnatural character had occurred. Although the *Myrmica ruginodis* population has remained approximately the same as in 1936, the fact that the number of nests has increased shows to some degree that this species is inclined to be in the ascendant. The reduction of the population of *A. flavus* may have played a part in this change.

Secondly, the repeated digging up of nests for observation hardly seems a success with *Acanthomyops flavus*. The great reduction in population of this species is not quite a natural event, I am afraid, but is due to the ants being disturbed. The two nests, which have existed through the three seasons, have decreased in population in the case of nest no. 1 from 5743 (1935), 1543 (1936) to 152 in 1937 and in the case of nest no. 3 from 5613 (1935), 2210 (1936) to 1481 in 1937. I found that in the case of nest 1 there had been considerable mortality since 1936. Possibly the ants of the two new nests, 21 and 27, have come into the area from the surrounding region.

With regard to the other two species of ants I feel that the method used in these surveys is quite suitable, partly owing to the movements of the ants from stone to stone, and there does not seem to be any mortality when returned to their nests. Artificial disturbances have not the same disastrous effects on them as on *Acanthomyops flavus*.

11. ACKNOWLEDGEMENTS

I wish to thank Mr H. St J. K. Donisthorpe for naming the ants; the Agent to the Savile Estate, Mr C. A. E. Horton, for renewing permission to use the land; Mr H. Wright, Principal of the Technical College, Dewsbury, for allowing me the use of the Balance Room in the Chemical Department; experts at the Natural History Museum, London, Mr Frederick Laing, aphides and Mr F. G. Westropp, Thysanura and Collembola; Dr T. W. Woodhead, grasses; and Mr Charles Elton for encouragement and suggestions.

12. SUMMARY

1. A survey of three species of ants living on a portion of a hillside at Thornhill, Yorkshire, was repeated in 1937, the object being to record the fluctuations of populations and biomasses.

2. *Territory.* No increase of territory of the two species *Formica fusca* and *Myrmica ruginodis* was observed. It was, however, found that *Acanthomyops flavus* does forage for food and attends the apterous viviparous females of the aphid *Tetraneura ulmifoliae*, which are on the roots of the grass *Holcus mollis*.

3. *Populations. Acanthomyops flavus* showed an increase of population due, no doubt, to immigration from surrounding regions. *Formica fusca* showed a decreased population from that of 1936, while that of *Myrmica ruginodis* was roughly the same.

4. *Densities of population. Acanthomyops flavus* showed the greatest economic density and *Formica fusca* the least. The lowest densities of the three species were in the same order.

5. *Weights and biomass.* After the census of each permanent nest had been made, the occupants were weighed and the biomass was found. From these calculations *Formica fusca* was found to have the greatest weight per sq. m. This was followed by *Myrmica ruginodis*. However, *Myrmica ruginodis* seems to be in the ascendant, as both in number of nests, in biomass and in actual weight it has shown increases on the 1936 figures.

6. The Thysanuran, *Campodia staphylinus*, was found abundantly under the stones and under stones covering the ants' nests, especially after rain, and the Collembolan, *Entomobrya multifasciata*, was found amongst the decaying layer of bracken, grass, etc., covering the area.

7. The method of repeated digging up of nests for censuses hardly seems suitable for determining the populations of nests of *Acanthomyops flavus*. The other two species seem to suffer less disturbance and mortality by it.

REFERENCES

1. **Carey, E. & Diver, C.** (**1937**). "Territory in the yellow field ant (*Acanthomyops flavus*)." J. Anim. Ecol. 6: 193–4.
2. **Theobald, F. V.** (**1929**). "The plant lice or Aphididae of Great Britain." Vol. 3: 299.
3. **Pickles, W.** (**1935**). "Populations, territory and interrelations of the ants *Formica fusca*, *Acanthomyops niger* and *Myrmica scabrinodis* at Garforth (Yorkshire)." J. Anim. Ecol. 4: 22–31.
4. **Pickles, W.** (**1936**). "Populations and territories of the ants, *Formica fusca*, *Acanthomyops flavus*, and *Myrmica ruginodis*, at Thornhill (Yorks.)." J. Anim. Ecol. 5: 262–70.
5. **Pickles, W.** (**1937**). "Populations, territories and biomasses of ants at Thornhill, Yorkshire, in 1936." J. Anim. Ecol. 6: 54–61.
6. **Elton, C.** (**1932**). "Territory among wood ants (*Formica rufa* L.) at Picket Hill." J. Anim. Ecol. 1: 69–76.
7. **Gause, G. F.** (**1934**). "The struggle for existence." Baltimore.
8. **Donisthorpe, H. St J. K.** (**1927**). "The guests of British ants." London.

CANADIAN ARCTIC WILD LIFE ENQUIRY, 1936–37[1]

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(*With* 4 *Figures in the Text*)

1. Introduction

This is the second report based on questionnaire enquiries into the annual changes of abundance of certain species of animals living in the Canadian Arctic and Labrador. The previous report should be consulted for a discussion of the species under investigation, the form of questionnaire used, and a full description of the methods of mapping replies. Fluctuations in abundance of the arctic fox (*Alopex lagopus*) are one of the vital factors in the economy of the Canadian North, affecting at the same time both the fur trade and native welfare. They are the practical aspect of a remarkable periodic oscillation in animal populations which in any case deserves study on account of its scientific interest. This oscillation affects also lemmings (*Lemmus* and *Dicrostonyx*) which form one of the chief food supplies of the arctic fox. It is the purpose of this enquiry to make as full a record as possible of the fluctuations, and if possible to correlate those of the fox with changes in its food supply, particularly lemmings, and also with climatic and other variables. The snowy owl (*Nyctea nyctea*) is also closely dependent upon lemmings, and its fluctuations may prove to be a useful index of the abundance of this basic food-animal, and therefore of fluctuations in the fur crop.

Outbreaks of epidemic disease among sledge dogs are another important factor in the life of the North. The possibility of correlation between these epidemics and mortality periodically affecting wild life is a fourth aspect being followed in this enquiry.

Questionnaires are sent out by the Northwest Territories Administration, Ottawa. Full co-operation has been given to the Bureau of Animal Population by the authorities, in particular by the Commissioner of the Northwest Territories, Dr Charles Camsell, and the Deputy Commissioner, Mr R. A. Gibson. The Governor and Committee of the Hudson's Bay Company have kindly allowed full use to be made of their annual zoological reports, and the Company's Fur Trade Commissioner in Winnipeg, Mr Ralph Parsons, and his staff, have given extensive co-operation. Mr Charles Elton has given me considerable help, and we wish to thank the many observers on the results of whose judgment this report is based.

[1] Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

Forty-six replies were received through the Government enquiry and sixty-five from Hudson's Bay Company posts in the Arctic. Information from the more southerly posts of the company has also been included in the case of the sledge dog. The enquiry is being continued.

2. Methods

The enquiry relies for its measure of changes in abundance upon opinions given by field observers, which are mapped by methods that have been made as objective and free from bias as possible. There is no doubt that these carefully standardized methods of mapping introduce very little distortion of the opinions expressed in the questionnaire replies. From the scientific point of view it is of greater importance to consider how far the observations made in the field are themselves liable to the errors that must necessarily enter into any subjective method of estimating changes in wild animal populations. Factors tending to reduce these errors are the great amplitude of the fluctuations observed, the year-to-year method of comparing abundance, and the fact that the observations are not only based upon individual experiences but in many cases also on those of other people, including native hunters familiar with wild life in the field. It is believed that the system of recording and mapping adopted is sufficiently reliable to give a substantially correct general picture of the wild life situation from year to year. It is in any case the only type of method at present applicable to the measurement of current biological phenomena over so huge an extent of country as the Canadian Arctic.

In Table 1 are listed the opinions of observers about abundance for the 12 months ending 31 May 1937, compared with the previous 12 months. The number of observers reporting "increase", "decrease" or "no change" is counted in each of the regions and summarized in Table 2 to give the main statistics for this report. The maps (Figs. 1, 3, 4) show the areas to which these reports apply. From the number of arrows indicating each kind of reply further statistics (Table 3) are obtained. These figures represent roughly the percentage area reporting "increase", "decrease" or "no change", each arrow representing an area of 2500 sq. miles. (For example, an area of 50 miles radius $=7900$ sq. miles gets 3 arrows $=7500$ sq. miles.)

When there are a number of adjacent areas from which similar reports are received it is possible to space the arrows so that their number gives a fair approximation to the total area involved. However, when no such unanimity is reached a regular pattern cannot be made and the approximation to the true area is less accurate. In this case the total number of arrows is counted and from it is subtracted a certain number of the arrows in disagreement, as shown in Table 3 by the small index figures. This may give a slight underestimate of the size of the area because an arrow is taken as contradicting another of different sign when there is any overlapping of the areas represented by the

two arrows. For this purpose these areas are considered to be strips "25 by 50 miles" along each side of the long axis.

The lemming reports in Group 9 may be taken as an example of the method of working out the percentage area covered by each type of observation. Here nine arrows are in disagreement: three of "decrease" contradicted by *three* of "no change", one of "decrease" contradicted by *one* of "no change" and *one* of "increase". The approximate area involved is therefore roughly 2500 sq. miles times the total number of arrows (eighteen) less *five*. Of this number, eight indicate "no change", but four are contradicted. The percentage by area reporting "no change" may therefore be expressed as between $\frac{4 \times 100}{13}$ and $\frac{8 \times 100}{13}$, or 31–62 %.

The advantage of such a method is that it gives a measure of the reliability of the observations. However, care must be taken to limit the weight given a single observer; and an arbitrary upper limit of ten arrows per person has been adopted. This limitation is achieved by spacing the arrows out from the centre of an area of large diameter. However in the case of one observer (No. 32 in Group 7) the area covered was not a solid block of country but several long stretches, mainly coastal. Here ten arrows have been spaced out over the area on the assumption that each represents an elongated area of 2500 sq. miles instead of a square. This procedure was less complicated than others to apply and also gives a probably less exaggerated representation of the area than would a closer spacing with more arrows. No such large areas were described in the previous report. Thus, while the maps are principally designed to convey a comprehensible diagrammatic picture, they have been constructed with the further aim of obtaining statistics on a basis of area covered.

Reports on "mice" are given by many observers, and where abundance or increase is stated this is listed but not mapped or analysed. Some of the lemming reports may perhaps refer to mice but this error is not considered serious. In any case both are an important source of food for predatory species.

It should be mentioned that the data have been treated as objectively as possible and no attempt has been made to cover up even obvious misstatements. This course is considered preferable to anything that would lay the results open to the criticism of being engineered. In two instances, however, some discretion has been observed in mapping the present data. In Group 1 (Northern Labrador) mapping has been confined to the coast as it is considered that the two larger areas described in the Hudson's Bay Company reports were meant to apply less to the arctic animals than to the other species also covered by the reports. In Group 2 it has been decided to omit the Fort McKenzie report from the calculations (though it has been mapped) since the other reports in this group all refer to phenomena on the coast or inland a distance mostly less than 70 miles. Thus the ten arrows allotted this post would have unduly

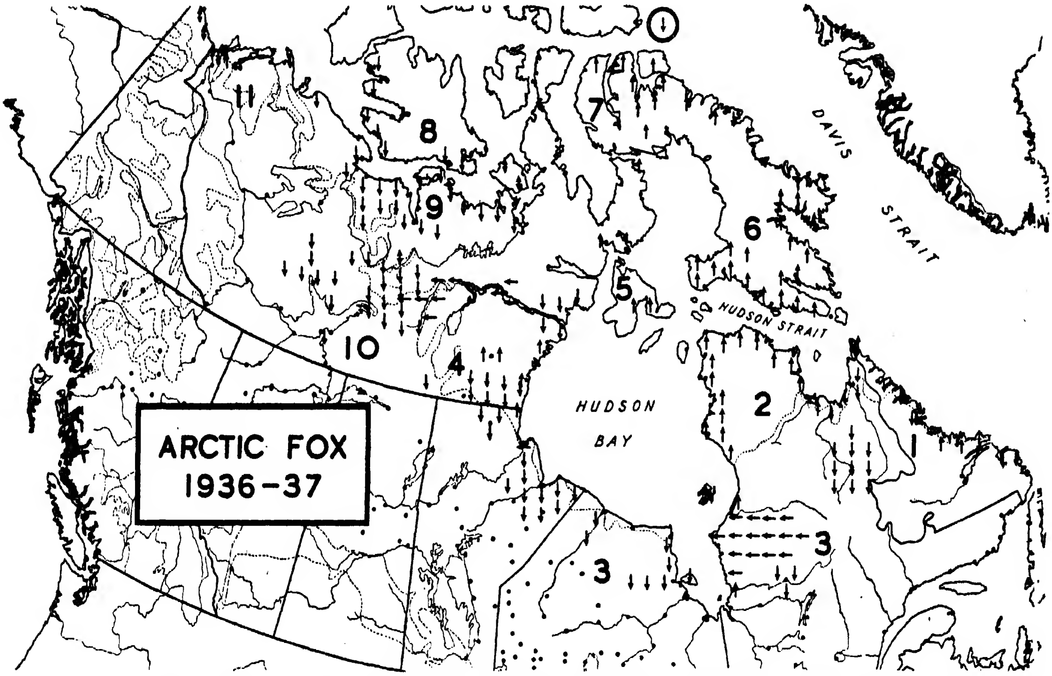

Fig. 1. State of the arctic fox population in 1936–37 compared with 1935–36. Arrows indicate the areas covered by observers reporting INCREASE (↑), DECREASE (↓), and NO CHANGE, NOT ABUNDANT (←). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

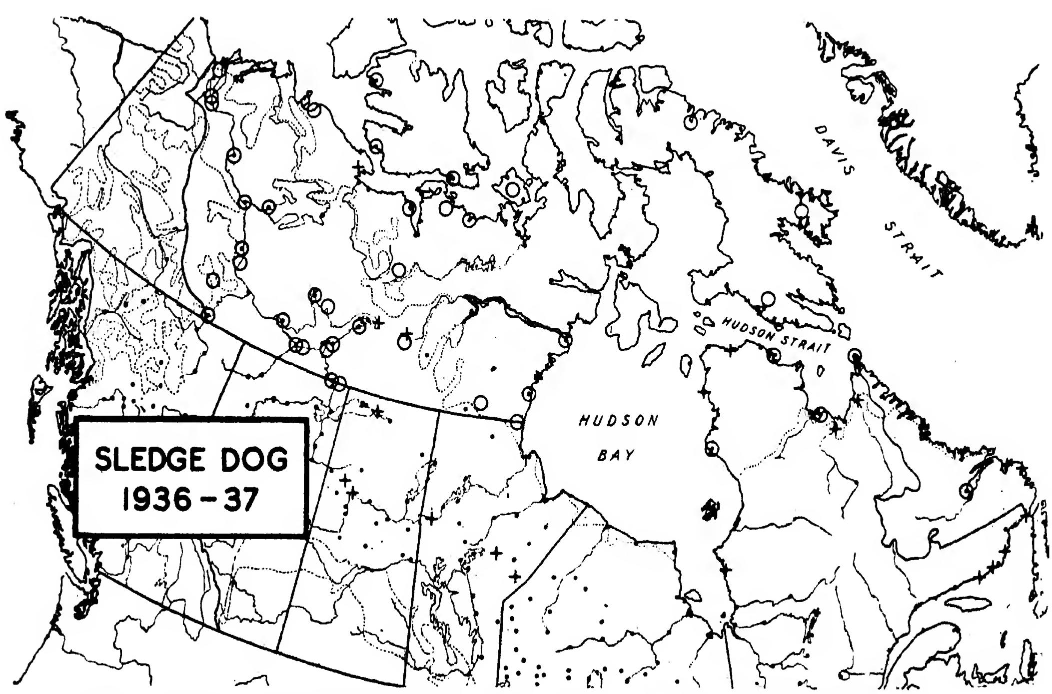

Fig. 2. Prevalence of disease among sledge dogs in 1936–37. Reports of disease are indicated +; disease absent or in minor proportions ○. Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones.

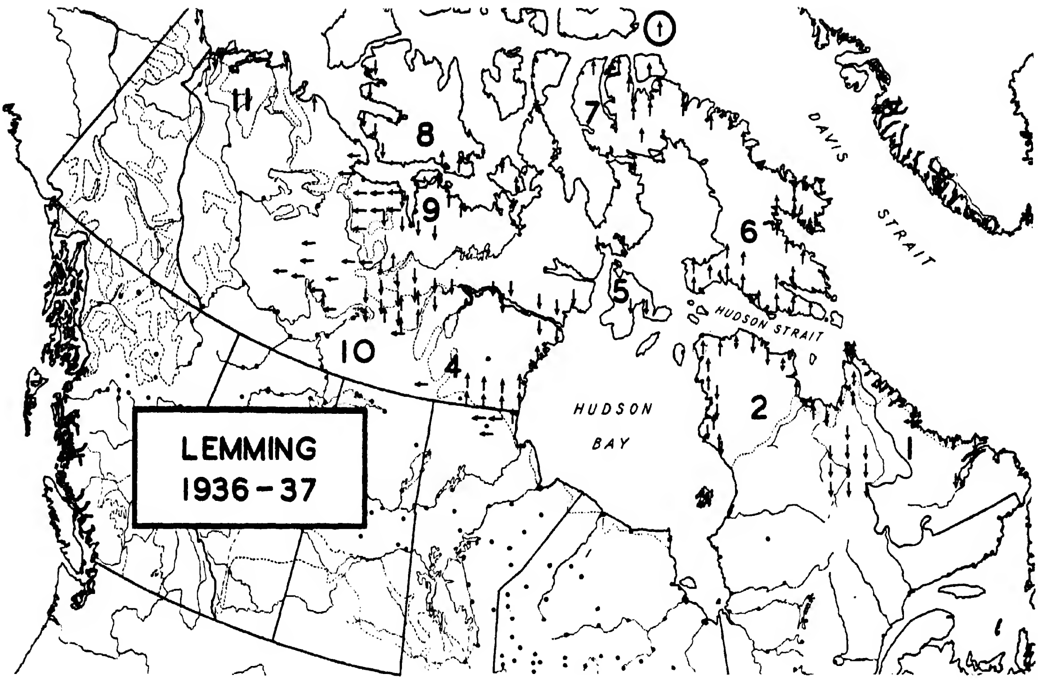

Fig. 3.

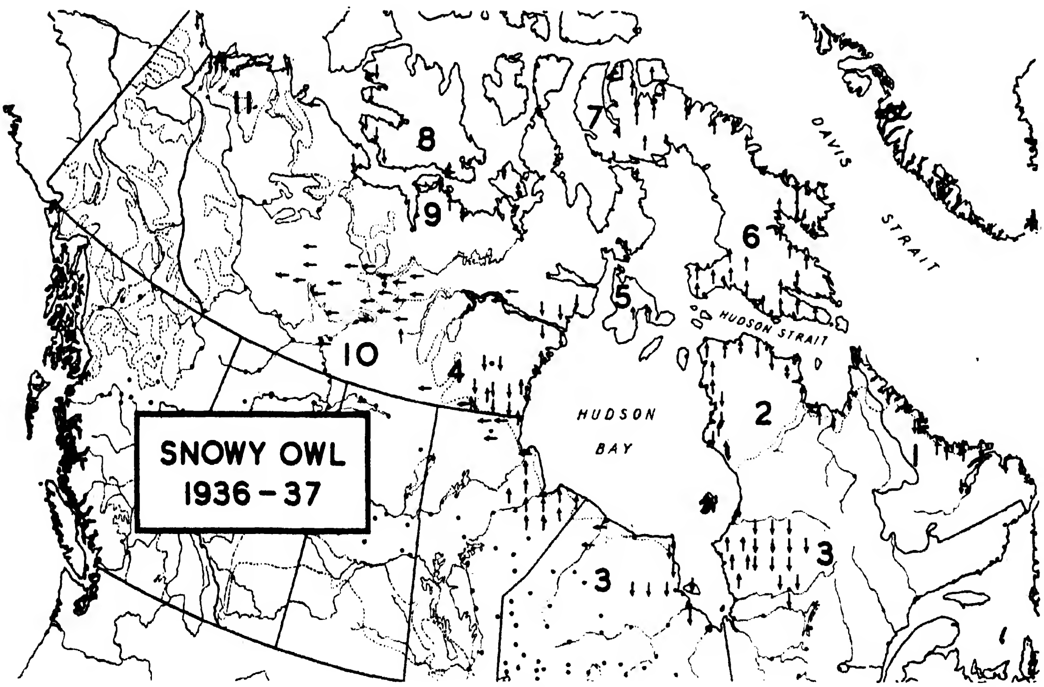

Fig. 4.

Figs. 3, 4. State of the lemming and snowy owl populations in 1936–37 compared with 1935–36. Arrows indicate areas covered by observers reporting INCREASE (↑), DECREASE (↓), and NO CHANGE, NOT ABUNDANT (←). Black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

influenced the results in this group. In any case lemmings were stated in a report for 1932–33 to be very scarce at all times round this post. In Group 3, south of the breeding range of the arctic fox, all the areas have been mapped in full.

In the maps of sledge dog reports (Fig. 2) a circle indicates that a definite report has been received of absence of serious disease, a plus sign that an outbreak has occurred as described in Table 4 (*a*). One sign only is given per observer except when two or more distinct localities are described. The Hudson's Bay Company observers are only asked to give details when disease is present: thus lack of a specific statement may be taken to imply that disease was absent, though actually no circle is put on the map.

3. Results

Lemming. The most striking feature of the 1936–37 results is the unanimity of reports of increase over the whole huge extent of Baffin Island. During 1935–36 there were only two such reports, in the south-eastern part of the island, so that a remarkable regional recovery is indicated. This upward trend of the lemming population was also shown, to a lesser extent, along the northern fringe of the Quebec Peninsula from Hebron in Labrador to Port Harrison in Hudson Bay. Although reports of continued scarcity or decrease came from several places, the contrast with 1935–36 is well marked. Increase among "mice" or lemmings or both was reported fairly commonly from James Bay and the south and west parts of Hudson Bay in 1935–36, and this increase was apparently well maintained in 1936–37: on the north-west side, as far as Tavane. North of this there was continued scarcity and decrease, and in Group 5 the increase previously reported was reversed.

In the Western Arctic no broad regional trends are apparent and the prevalent scarcity from 1935–37 undoubtedly made comparisons extremely difficult. It should be noted, however, that in the vicinity of King William Island and Cambridge Bay and the mainland south of these points, lemmings were reported well on the increase. This is confirmed by some later information reaching Cambridge Bay by dog team on 19 June from the post manager at King William Island: "Lemming and mice in immense numbers crossing from mainland to islands northward. Thousands were drowned on the ice crossing over" (Postscript to report No. 30).

Elsewhere in the West there was scarcity of lemmings, correlated with scarcity of arctic foxes and snowy owls. A notable exception was Baillie Island: "It was only in late April and early May that there was any great number of both white foxes and coloured foxes in this locality. The white foxes were coming in off the ice in May steadily, more than in any other spring that we remember. Perhaps they were following the lemming, whose tracks (and often the animals themselves) could be seen even for miles out on the ice. The

land was overrun with them. The snowy owl can be seen everywhere, sitting on the tops of knolls, and the natives report that many of the nests have as many as fifty dead mice scattered around them."

A further report (No. 31) may be quoted as showing some of the difficulties of making exact reports for large areas:

Thelon Game Sanctuary. In a considerable area in which lemming were scarce last year they were more abundant (western portion). In certain parts of this region where they were abundant in 1935 they are now less so. In the eastern region (towards Baker Lake) many patches of abundance were left though there were signs of a heavy decline in many places not long previous to this summer. I was told that many bodies were to be seen at break-up at Baker Lake. After break-up I noted windrows of lemming dung on the shores of Aberdeen and Shultz Lakes—which are hard to explain unless the animals were on the lake ice and on the Thelon river ice in numbers.

Arctic fox. In 1935–36 no less than 91% of all observers reported decrease, and only 4% increase. In 1936–37 a considerable difference appeared between Eastern and Western Arctic reports and it has been necessary to consider them separately. In the East, 57% of observers reported increase, and this was particularly noticeable in Baffin Island and along the coast of Northern Quebec. The increase was stated at Diana Bay to have been "about 6 : 1, a rather surprising increase over last year".

There is only small evidence of increase elsewhere in Hudson or James Bay, especially outside the breeding range of the arctic fox, south of the tree limit. However, it must be pointed out that there was only one report of increase (in Group 1) from the whole of the Eastern Arctic in 1935–36 so that a definite improvement is indicated. In the Western Arctic only 11% of observers claimed that increase had taken place, and these reports were almost entirely contradicted, for by area the increase was only 2–13%. Report No. 41 (Group 11) states: "It is thought by local trappers that white foxes are now definitely on the increase in this area. The increase is slow but steady, although a sudden increase might occur at any time, not from breeding in the district but by the arrival of a migration, probably from arctic islands, under suitable conditions of ice."

Snowy owl. There is again remarkable unanimity in the reports of increase from Baffin Island, and this, like the increase in foxes, seems to be correlated with an increase of lemmings.

Baffin Island, south coast (No. 27). An Eskimo said he had seen seven snowy owls in one day, in the vicinity of Markham Bay in October 1936. This is an unusually large number to be seen in one day on any part of the south coast of Baffin Island.

A further correlation exists between reports of increase of lemmings and snowy owls along the coast between Hebron and Port Harrison. Out of ten reports of lemming increase no less than eight were accompanied by similar reports of increase for the snowy owl. Owls were scarce in the southerly Group 3 and had

not increased on the west coast of Hudson Bay as much as the 1935–36 reports might have led one to expect. Increase on Southampton Island was apparently not correlated with increase in lemmings; but from the King William Island–Cambridge Bay vicinity, although some conflicting reports were received, increase seems to have accompanied an increase in lemmings, though it was perhaps of a patchy nature. Farther west, except in the vicinity of Baillie Island, there seems to have been a great scarcity of snowy owls for another year.

Sledge dog. Sledge dogs appear to have been comparatively free from disease in the Arctic during 1936–37. However, there have been outbreaks along the coast of Northern Quebec, though none of a very extensive nature. Three reports from the Western Arctic were couched in rather general terms so that it is not certain that they referred to the period under consideration.

It has been decided to extend the area covered by the enquiry to all of the Hudson's Bay Company posts reporting "dog sickness". The results show that there were several severe outbreaks of distemper in parts of Northern Manitoba and Saskatchewan and in the eastern corner of Quebec Peninsula.

Table 1. *Summary of original data on arctic fox, lemming, snowy owl and sledge dog (part) for* 1936–37

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, r. = rare, s. = scarce, × = not noticeably scarce or abundant, a. = abundant, v. = very.

Sledge dogs: 0 indicates a report that disease was entirely absent. $0^{3,8}$ = report of disease in minor proportions as specified in Table 4 (*b*). + = prevalent disease as specified in Table 4 (*a*). Bracketed observations in the sledge dog column are represented by the same symbol in the map. One symbol is given each observer except where indicated (2).

Square brackets indicate observations that have been partly or entirely omitted from either the map or the calculations—see text.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received directly from the Hudson's Bay Company.

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
	Group 1. Northern Labrador coast					
	Frenchman's Island, outside islands and 30 miles inland	D. s.	—		D. s.	$+^1$
	Cartwright	D. v.s.	—		D. v.s.	$+^2$
	Rigolet: half-way to Cartwright; half-way to Makkovik; one-third way to Northwest River	D. v.s.	D. v.s.		D. v.s.	—
	Northwest River [and inland 400 miles by trappers' reports] ...	r.	D. v.s.		D. v.s.	0^3
	Makkovik, 30 miles north and south [and 100 miles inland from head of bays]	I.	—		I.	—
	Hopedale and 30 miles radius ...	I. ×	—		I. s.	—
	Davis Inlet and 30 miles radius ...	N. s.	—		I. s.	—
	Nain and 35 miles radius	D. v.s.	N. s.		D. v.s.	—
	Nutak	D. v.s.	s.	a.	D. v.s.	—
	Hebron and 50 miles radius ...	D. s.	I. a.	I. a.	D. s.	—
	Port Burwell	I.	I. a.	I. v.a.	I.	—
34.	Port Burwell	I. ×	N. ×		v.s.	0

Table 1 (*cont.*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
	Group 2. Coast of Northern Quebec, south to Richmond Gulf and inland					
	Georges River and 50 miles radius	D. s.	I.	I.	—	+[4]
	Whale River to Georges River ...	D. s.	D. s.		D. v.s.	—
	Fort Chimo and 25 miles radius ...	D. v.s.	D. ×		D. ×	+[5]
	[Fort McKenzie and 120 miles radius]	[D. v.s.]	[D. v.s.]	I.	—	—
	Leaf River and coastal area between Payne and Koksoak Rivers ...	I. ×	I. a.	I. a.	I. ×	0
	Payne Bay to Hopes Advance Bay and Aupalook Bay	I. ×	I.		I. ×	—
	Diana Bay, the islands, coast and inland 60 miles	I. ×	I. ×		I. ×	—
	Stupart Bay, west to East Sugluk, south to Diana Bay	I. s.	D. s.		D. s.	0
	Sugluk West and 60 miles radius ...	I. ×	I. a.	I. a.	I. ×	+[6]
	Wolstenholme; 30 miles east and 120 miles south	I. ×	I. a.		I. a.	—
	Cape Smith, inland 50, south 20 and north 70 miles	I. ×	I. ×		I. ×	+[7]
	Povungnetuk and 60 miles radius ...	I. ×	D. s.		D. s.	—
	Port Harrison and 70 miles radius...	I. ×	I. ×		I. ×	—
28.	Port Harrison district, from Kogatuk Bay on the north to Broughton Island	I. ×	D. ×		D. ×	0
	Group 3. South parts of Hudson Bay, James Bay and inland					
	Belcher Islands	I. s.	—		I. s.	—
	Great Whale River north to Richmond Gulf	I. s.	—	I. a.	D. s.	—
	Fort George and 100 miles radius ...	N. v.s.	—		I. v.s.	—
	Kanaapuscow, north, west and south 100 miles; east approx. [800 miles]	N. s.	—	I.	D. v.s.	—
	Eastmain	I. s.	—	I.	—	–
	Neoskweskau and 50 miles radius ...	D. s.	—		D. s.	—
	Albany; 50 miles south, 20 miles north and 40 miles from coast ...	—	—	I.	D.	—
	Attawapiskat; south to the Lawashi River, 150 miles inland, north to Cape Henrietta Maria and Agamiski Island	D. s.	—	I. a.	D. s.	—
	Severn and 100 miles inland ...	D. s.	—		N. ×	—
	York Factory and 120 miles radius	D. s.	—	I. a.	I.	—
	Group 4. West coast of Hudson Bay, north from Nelson River					
	Churchill and 50 miles radius ...	N.	—		N.	—
	Caribou and 50 miles radius ...	D. s.	N. ×		N. ×	—
	Nonala and 20 miles radius... ...	I. ×	I. ×		I. ×	—
5.	Lat. 60°–61° 15′ and from west coast of Hudson Bay to east side of Nueltin Lake	D. v.s.	I.		D. ×	—
	Cape Churchill to Eskimo Point; inland to Windy Lake	—	—		—	0
8.	Lat. 60°–61° and between Nueltin Lake and Sadiah Lake (100 miles west of Hudson Bay coast) ...	s.	I. ×	v.a.	I. s.	0
	Nueltin Lake	D. v.s.	I. v.a.	I. v.a.	N.	—
	Stony Rapids, north-east of, at Snowbird Lake	D. s.	N. s.		N. ×	—
17.	Eskimo Point	I. a.	—		s.	0
	Eskimo Point and 40 miles radius ...	I. ×	I. v.a.	I. v.a.	I.	0
	Padley and 40 miles radius	I. a.	—	I. a.	D. s.	—
	Tavane and 50 miles radius ...	I. ×	I. a.	I. a.	I. ×	—
	Chesterfield to Cape Fullerton; south to Rankin Inlet and 100 miles inland	D. s.	D. s.		D. s.	0
	Baker Lake and 50 miles radius ...	N. ×	D. ×		N. ×	—

Table 1 (*cont.*)

		Arctic fox	Lemming ["Mice"]	Snowy owl	Sledge dog
	Group 5. Southampton Island and Repulse Bay				
	Repulse Bay and radius of 5 miles...	I. ×	D. s.	×	—
	Southampton Island: south Bay ...	I. s.	D. s.	I. a.	—
	Group 6. Southern Baffin Island				
	Lake Harbour east to Pritzler Harbour, west to west side of Markham Bay (native reports)	I. v.s.	I. ×	I. ×	—
27.	Eastern end of Frobisher Bay to Nuwata, Foxe Peninsula, on the south coast of Baffin Island	I. v.s.	I. ×	I. ×	0
	Cape Dorset; Foxe Peninsula east to Amadjuak Lake; north to south end of Nettilling Lake	I. ×	I. ×	I. ×	—
	Frobisher Bay, south-east to Waddell Bay, north-east to Sylvia Grinnell River, down west side of Bay to Newell Sound	I.	I. s.	I.	—
33.	Pangnirtung Fjord and other areas adjacent to Cumberland Gulf ...	I.	I. a.	I. a.	0
	Pangnirtung Fjord and Cumberland Sound	I. ×	I. ×	I. ×	—
	Group 7. Northern Baffin Island and north				
	Clyde and 35 miles radius	D. ×	I.	I.	—
32.	Pond's Inlet, south to Home Bay, south-west to Igloolik, north-west to Arctic Bay; south shore Bylot Island	I. a.	I. v.a.	I. ×	0
	Pond's Inlet, Eclipse Sound and inland south-west	I. ×	I. ×	I. ×	—
	Arctic Bay and north coast of Baffin Island	I. v.s.	I. ×	v.s.	—
	Craig Harbour, Ellesmere Island ...	D. v.s.	I. v.s.	v.s.	0
	Group 8. Boothia Peninsula and islands west				
	King William Island and vicinity ...	D.	I.	I. v.a.	—
39.	King William Island*	I. ×	I. ×	D. s.	0
40.	Cambridge Bay vicinity, Victoria Island	D. v.s.	I. a.	N. ×	0
36.	{ Cambridge Bay and 50 miles radius	D. v.s.	I. v.a.	—	— }
	{ Cambridge Bay only	—	—	I. v.a.	0 }
	Reid Island and from Lady Franklin Point to north shore of Prince Albert Sound	D. v.s.	D. v.s.	D. v.s.	0
	Fort Collinson, Walker Bay, north to Deans Dundas Bay, south to Minto Inlet	D. s.	D. s.	D. s.	0
	Group 9. Adelaide Peninsula, west to Coppermine River, and inland to Back River				
39.	Mainland around mouth of Perry River*	[I. ×]	[I. ×]	[D. s.]	0 (2)
30.	{ Back River to Cambridge Bay ...	D. s.	—	—	—
	{ Perry River district to Cambridge Bay	—	I. v.a.	I.	0[8]
	Bathurst Inlet and inland for 100 miles east and west	D. s.	D. s.	—	—
38.	Baillie Bay, Arctic Sound	D. v.s.	D. ×	×	0
	Kugaryuak and inland to Red Rock Lake [and Napaktolik]; east to Burnside River	D. s.	N.	—	—

* The same observer is not included in more than one group in Table 2.

Table 1 (*cont.*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
3.	Back River, Beechey Lake, Musk-ox Lake and Fry Lake districts ...	I. ×	I. ×		×	0
21.	North of west end of Aylmer Lake	D. v.s.	D. ×		D. v.s.	—
	Fort Reliance	—	—		—	0
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
31.	Thelon Game Sanctuary. (For lemming: western portion of Sanctuary, I; eastern portion, D)	N.	* I. / D		—	—
9.	Ptarmigan Lake, Clinton Colden Lake	N. s.	D. v.s.		N. ×	—
	Fort Reliance	—	—		—	0
15.	Lynx Lake, headwaters Thelon River, Reliance district	D. v.s.	N.		I. v.a.	0
22.	Whitefish Lake—east to [Granite Falls] on Thelon River	v.s.	I. s.		s.	+[9]
7.	Lat. 62°–65° and Long. 104°–110°, excluding Thelon Game Sanctuary ...	D.	—		r.	—
	North-east of Reliance to Thelon Game Sanctuary thence south-east to Whitefish Lake, thence west to Reliance	—	I.		—	—
	Snowdrift and Reliance	—	—		—	0 (2)
	Snowdrift and between Lat. 62°–65° and Long. 105°–111°	D. v.s.	D.		N.	0
11.	East end of Great Slave Lake ...	D. v.s.	—		v.s.	+[10]
23.	Resolution district and Slave River Preserve	D. v.s.	—		N. s.	0
45.	Yellowknife River, north shore of Great Slave Lake	—	I. v.a.	I.	—	0
37.	Yellowknife Bay and radius of 40 miles north and east	—	N.		v.s.	0
	Fort Rae, south-east to Yellowknife River, west to Indian village on Grandin River entering Lac La Marte, north-east to Snare Lake district, north to Hottah Lake ...	D. v.s.	—		v.s.	—
24.	Fort Rae to Snare Lake, Providence Lake and Lac de Gras; to Hottah Lake; to mouth of Grandin River, and to Gros Cap	D. v.s.	N. s.		N. s.	0
	Group 11. Coppermine River to Alaska					
	Coppermine, 50 miles east, west and south	D.	N.		s.	—
29.	Basil Bay and 50 miles radius in Coronation Gulf	D. v.s.	N. s.	v.a.	D. s.	+[11]
43.	From Tuktoyaktuk east along the coast to Pearce Point	D. v.s.	I. v.a.		N.	0
	Baillie Island and vicinity	D.	I. a.		I. a.	—
	Aklavik and lower delta of Mackenzie	D. s.	D. s.		I. ×	—
41.	Mackenzie River delta [south to Point Separation], west to Herschel Island and east to Richards Island ...	I. s.	—	a.	D. v.s.	0
	Herschel Island west to Shingle Point	D.	D.		D.	—

* Observer's vote is halved (Table 2).

Table 2. *State of arctic fox, lemming and snowy owl populations in* 1936–37. *Number of observers reporting relative abundance compared with* 1935–36

	Eastern Arctic									Western Arctic					
Group No. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	4	10	3	5	2	6	3	33	**57**	1	1	—	1	3	**11**
Decrease	6	3	4	5	—	—	2	20	**34**	5	5	7	6	23	**82**
No change	1	—	2	2	—	—	—	5	**9**	—	—	2	—	2	**7**
	11	13	9	12	2	6	5	58	**100**	6	6	9	7	28	**100**
Lemming:															
Increase	2	8	—	6	—	6	5	27	**64**	4	2	3½	2	11½	**43**
Decrease	2	5	—	2	2	—	—	11	**26**	2	3	2½	2	9½	**35**
No change	2	—	—	2	—	—	—	4	**10**	—	1	3	2	6	**22**
	6	13	—	10	2	6	5	42	**100**	6	6	9	6	27	**100**
Snowy owl:															
Increase	4	7	3	4	1	6	3	28	**52**	2	1	1	2	6	**32**
Decrease	7	5	5	3	—	—	—	20	**37**	3	1	—	3	7	**36**
No change	—	—	1	5	—	—	—	6	**11**	1	—	4	1	6	**32**
	11	12	9	12	1	6	3	54	**100**	6	2	5	6	19	**100**

Table 3. *State of arctic fox, lemming and snowy owl populations in* 1936–37. *Number of arrows indicating relative abundance compared with* 1935–36.

	Eastern Arctic									Western Arctic					
Group No. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	3^{1}	15^{1}	3^{2}	5^{2}	3	19	12^{1}	60^{7}	**45–50**	2^{2}	2^{2}	—	4^{3}	8^{7}	**2–13**
Decrease	6	4^{1}	18^{2}	19^{3}	—	—	2^{1}	49^{7}	**35–41**	9^{2}	19^{2}	21^{3}	7^{3}	56^{10}	**77–93**
No change	1^{1}	—	15^{4}	4^{1}	—	—	—	20^{6}	**12–17**	—	—	6^{3}	—	6^{3}	**5–10**
	10^{1}	19^{1}	36^{4}	28^{3}	3	19	14^{1}	129^{10}		11^{2}	21^{2}	27^{3}	11^{3}	70^{10}	
Lemming:															
Increase	2^{1}	12^{7}	—	10^{2}	—	19	14	57^{10}	**62–75**	4	4^{1}	6^{5}	2	16^{6}	**20–32**
Decrease	2	10^{7}	—	8	3	—	—	23^{7}	**21–30**	5	6^{4}	12^{4}	3	26^{8}	**36–52**
No change	2^{1}	—	—	4^{2}	—	—	—	6^{3}	**4–8**	—	8^{4}	9^{2}	2	19^{6}	**26–38**
	6^{1}	22^{7}	—	22^{2}	3	19	14	86^{10}		9	18^{5}	27^{6}	7	61^{11}	
Snowy owl:															
Increase	4	10^{6}	13^{2}	8^{5}	2	19	12	68^{13}	**48–59**	3^{3}	3^{1}	1^{1}	2^{1}	9^{6}	**8–24**
Decrease	7	10^{6}	21^{2}	14^{5}	—	—	—	52^{13}	**34–45**	7^{2}	2^{2}	—	5^{1}	14^{5}	**24–37**
No change	—	—	2	9^{4}	—	—	—	11^{4}	**6–10**	1^{1}	2^{1}	18^{1}	1	22^{3}	**33–58**
	11	20^{6}	36^{2}	31^{8}	2	19	12	131^{16}		11^{3}	7^{2}	19^{1}	8^{1}	45^{7}	

The index figures in lines 1–3 under each species show the no. of conflicting arrows; in line 4 the no. to be subtracted from the totals in calculating percentages.

Table 4. *Details of disease among sledge dogs*, 1936–37.

Numbers indicate that the full description of an area has already been given and is to be found opposite the corresponding small number in the last column of Table 1.

(*a*) *Disease or epidemic prevalent* (+ on map).

Quebec and Labrador.

Natashquan. "Quite a few dogs died of unknown disease in the fall of 1936."

Romaine. "This year considerably fewer dogs succumbed to disease than last year."

Mutton Bay. "Distemper killed from 60 to 75% of the sledge dogs."

Blanc Sablon. "All sledge dogs in this vicinity had distemper, commencing late in February and still prevalent. Almost all have died with the disease. It spread from the east."

1. *Frenchman's Island.* "During the month of January the south section of the coast was stricken by an epidemic among the dogs, which lasted up to about the middle of March. When the dogs were taken sick they would cough, fall and stay down for about 15 minutes, then get up, go round in a circle about ten times, and go in a straight line very fast. Soon after they would die."

2. *Cartwright.* "A dog epidemic appeared in Cartwright during the early winter and destroyed practically all the teams. It also spread southward, causing destruction to the dogs. The northern teams were spared by prompt measures being taken to stop all teams from this section from going north. The symptoms took different forms: some dogs went mad, others went blind and had distemper, while others would not eat and wasted away. In some cases there appeared to be acute abdominal pain and leg cramp. A larger percentage of dogs died during this epidemic than in any other that has appeared among the dogs."

4. *Georges River.* "A number of dogs have been sick this spring. Symptoms: frothing at the mouth and staggering. Some died but the majority recovered."

5. *Fort Chimo.* "Several sledge dogs are reported to have died."

6. *Sugluk West.* "Epidemic in February and March: violent and painful diarrhoea, loss of appetite. Only fatal in cases underfed previously."

7. *Cape Smith.* "Disease noticed in early winter. Symptoms: contraction of stomach muscles, loss of walking powers."

N.W. Territories.

9. *Whitefish Lake.* "Disease in May. Pus in eyes and nose—especially pups. Also found in lungs."

10. *East end Great Slave Lake.* "Some disease in April and May. Symptoms: running at nose, loss of flesh—no food; death usually follows."

11. *Basil Bay.* "Disease appeared in February and March. Symptoms: large pockets of pusy fluid breaking out almost anywhere on the dog. Most dangerous for young dogs and pups."

Manitoba.

Island Lake. "Practically all sledge dogs died during winter. Heavy discharge from eyes and nose, stomach trouble."

Oxford House. "Sickness amongst the dogs prevailed in the entire district during the winter. Many died."

Pukatawagan. "Great numbers of sledge dogs have died of distemper this spring."

Saskatchewan.

Pine River. "Distemper made great havoc among the dogs of the entire area in early winter."

Clear Lake. "Disease among sledge dogs from July 1936 until December 1936, about 20% of the dogs in this locality died off."

Fond du Lac. "Considerable amount of paralysis in hind legs; blood passed with urine."

(*b*) *Isolated cases of disease* (0 on map, but qualified as below).

Labrador.

3. *Northwest River.* "A few dogs around the Bay suffered from 'dog sickness' but it was not of a violent character here as very few, if any, died from it."

N.W. Territories.

8. *King William Island.* "Two cases of glandus rabies."

Table 4 (*cont.*)

(*c*) ***Disease absent*** (0 on map. When more than one symbol is given this is stated (2) or (3)).

N.W. Territories.

26 miles east of Fort Smith.

Fort Smith district. 60th parallel to east boundary of Wood Buffalo Park and south-eas boundary of Slave River preserve, north-east to Nonacho Lake and south to 60th parallel.

Mouth of Big Buffalo River.

Providence and Hay River (2).

Fort Providence and up Horn River to Horn Mountains.

Fort Providence.

Liard River.

South Nahanni valley and south fork for about 100 miles.

Willow River district, 125 miles down river from Fort Simpson.

Wrigley, Norman and Franklin (3).

Good Hope.

Arctic Red River.

Point Separation and Arctic Red River (2).

[*Cape Perry,* via Aklavik.]

4. Summary

1. This is the second annual report of an enquiry into population trends of lemmings (*Lemmus* and *Dicrostonyx*), the arctic fox (*Alopex lagopus*) and the snowy owl (*Nyctea nyctea*) in the Canadian Arctic. The enquiry was promoted by the Northwest Territories Administration of the Canadian Government, in co-operation with the Hudson's Bay Company, and mapped in the Bureau of Animal Population at Oxford.

2. Replies were received from 111 observers in the North, also from certain Hudson's Bay Company posts outside the Arctic, and the results are shown on maps giving a comparison with the season 1935–36, and analysed in a series of statistics which include allowance for the areas covered by different observers.

3. In the Eastern Arctic there was considerable increase reported in arctic foxes, especially on Baffin Island and the coast of Northern Quebec. Lemmings and snowy owls, which had begun to recover from scarcity in the previous season, showed further well-marked increase in the same region, and also to some extent elsewhere.

4. In the Western Arctic there were very few signs of such recovery among any of the species studied.

5. Details about disease among sledge dogs were also obtained, both from the Arctic and from certain more southerly posts. Several teams suffered heavy losses in the Eastern corner of Quebec Peninsula, while less severe outbreaks occurred along the coast of Northern Quebec. In the Western Arctic there was little disease in the North, but severe outbreaks were reported from Northern Manitoba and Saskatchewan.

6. Information about the numbers of ptarmigan was again received, but reserved for future analysis. The enquiry is being continued.

REFERENCE

Chitty, D. & Elton, C. (1937). "Canadian Arctic wild life enquiry, 1935–36." J. Anim. Ecol. 6: 368–85.

A. E. BOYCOTT

AN APPRECIATION

By E. J. SALISBURY

By the death of Arthur Edwin Boycott, at the early age of sixty-one, science has lost a distinguished pathologist and a naturalist of outstanding ability, whilst, for those who knew him well, there has passed from the scene a rich and scholarly personality whose friendship it was a privilege to enjoy.

The second son of a Hereford solicitor, Boycott was born in a district wealthy alike in its geological diversity and in the variety of its flora and fauna. Moreover, about the time that he was attaining maturity the Woolhope Club was at the zenith of its activity in the study of Natural History. On the excursions of the Club, Boycott, whilst still at the Cathedral School, came in contact with kindred spirits and particularly E. A. Bowles, who interested him in the Mollusca. At the age of seventeen he published a catalogue of the snails of Herefordshire, and this was the prelude to a lifelong interest in the subject of geographical distribution which in later years led to his editing the Roebuck Memorial number of the Conchological Society (1921), in which the data collected by W. Denison Roebuck were embellished by distribution maps, of all the British land and fresh-water Mollusca, which had been prepared by Boycott.

From Hereford Boycott went to Oriel College as a classical scholar and subsequently to Brasenose whence he obtained a first in the Natural Science Honours School. He subsequently went to St Thomas's Hospital and later to the Lister Institute.

From 1912 to 1915 he occupied the Chair of Pathology at Manchester University, where he came in contact with that peerless field naturalist, Charles Oldham. In 1915 Boycott was appointed to the Graham Professorship of Pathology in the University of London, tenable at University College Medical School, and at the same time came to live at Radlett.

In his new environment he quickly became an active member of the Hertfordshire Natural History Society and a regular attendant at its meetings, which were enriched by his gift for discussion and enlivened by his whimsical humour. At this time the H.N.H.S. included amongst its active members Dr Cook, the authority on Radulae, whilst C. Oldham, with whom the writer was privileged to serve as joint Hon. Secretary, was now as distinguished an authority on the Mollusca, especially that critical genus the *Pisidia*, as upon the habits of British birds. Boycott thus enjoyed the stimulus of sympathetic contacts and found time not only to pursue his professional duties and to edit

devotedly for more than a quarter of a century the *Journal of Pathology*, but to extend his studies of the habits and distribution of snails. The latter led him in 1918 to deliver as his Presidential Address to the Hertfordshire Society an account of the fresh-water Mollusca of the parish of Aldenham. This paper is a tribute alike to his industry and scholarship as also to his love of numbered paragraphs and footnotes. Some years later this account was supplemented by the results of further study in a second paper, and his Presidential Address to the British Ecological Society in 1933 was an extension of the same theme.

Boycott's tall figure, lean almost to emaciation, and clear-cut features were no more striking than his colourful personality. A man of strong views strongly held, he regarded any sort of compromise in respect to these as a betrayal of principle, though it were to the detriment of the causes which he espoused. To those who chiefly encountered his prejudices the marked capacity he had of exercising balanced judgement on scientific matters sometimes came as a surprise, whilst the very human and essentially kindly disposition beneath, that never spared itself in the service of others, was apt to remain unsuspected.

Boycott was at his best and happiest when tramping the country, which he loved with a discriminating appreciation, clad in an old suit of clothes and canvas shoes that, as he himself would put it, allowed water to drain away as fast as it had entered, and armed with a snail scoop. Thus equipped, with a tacit agreement to avoid the more controversial topics, he was the most delightful and charming of companions, as ready to learn as to impart, and as ready to apprehend phenomena of which he knew little as those of which he knew much.

Boycott's contributions to pathology were both numerous and distinguished, whilst his biological researches were no less able, but it was perhaps his passion for knowledge and his marked capacity to visualize it as a whole, rather than as so many abstractions, that marked him out from so many of his contemporaries.

REVIEWS

THE JOURNAL OF ECOLOGY
(Vol. 26, No. 2, August 1938)

THIS number opens with an appreciation (by E. J. Salisbury) of the character and work of the late Prof. A. E. Boycott.

The scientific contributions include a number of papers on algal ecology. In one of these, E. M. Lind deals with the periodicity of Algae in Beauchief ponds with reference to the seasonal changes in the solutes dissolved in the waters. E. A. Flint gives a preliminary account along similar lines of the periodicity of phytoplankton in Lake Sarah, New Zealand; while M. B. Hyde contributes records of seasonal variations in photosynthesis by the seaweed, *Fucus serratus*, kept under laboratory conditions for a year.

There are two detailed studies of plants in relation to their environment. G. H. Heath and L. C. Luckwill describe the rooting systems of certain heath plants with reference to the stratification and aeration of the soil; and H. G. Wager deals with the growth and survival of plants in the Arctic in connexion with the problem of the origin of *fjaeldmark*. Along similar lines is a short note by G. H. Bates on the characteristics of the plants of grass verges and paths.

On much wider lines is a general account of the island of Pabbay (on the west coast of the Outer Hebrides) by Charles Elton. This deals with the historical and ecological problems and with both flora and fauna.

Two papers on the Potterne Transplant Experiments of the British Ecological Society are contributed by E. M. Marsden-Jones and W. B. Turrill. One of these is the fifth of the biennial reports on the progress of this work, while the second summarizes the results obtained after ten years, 1928–37.

Three other papers deal in detail with habitat factors. W. H. Pearsall continues the papers on the soil complex in relation to plant communities, with a description of the characteristics of British moorland and bog soils having particular reference to their acidity. R. D. Misra gives the results of a detailed study of the edaphic factors controlling the distribution of aquatic plants in the English Lakes. A paper of very general application is one by R. E. Moreau reviewing the bases of climatic classification for biological purposes, with particular reference to East Africa.

Interest in the statistical study of vegetation continues, and in this number, B. N. Singh and K. Das analyse the distribution of weed species on arable land.

Reviews deal with the *Journal of Animal Ecology*, and with recent books on plant ecology.

W. H. PEARSALL.

ECOLOGICAL TERMS

J. Richard Carpenter (1938). *An ecological glossary.* 306 pp. with 12 appendices, including 6 maps. University of Oklahoma Press, Norman, Oklahoma, U.S.A. Price $4.

Mr Carpenter has attempted a compilation of which the rapidly growing study of ecology stands badly in need. That he has not been entirely successful is hardly surprising in view of the many problems with which the whole subject of ecological nomenclature bristles. But he has made a brave attack which will be of undoubted use, and may form the basis of a future more satisfactory work. Many will probably be irritated by the number of minor blemishes which could well have been avoided by more careful checking, and the reader gets the impression that the whole has been put together with too much haste.

Nevertheless, the book brings together into a handy form a great deal of otherwise widely scattered matter; and those who wish to render important service to their subject by ensuring the correct usage of words and avoiding the unnecessary multiplication of synonyms or neologisms will often be saved much time and trouble by referring to it. The reviewer has already had occasion to be grateful to Mr Carpenter. The appendices include some useful tables and maps.

From its nature, ecology can hardly be considered as a single subject that can be confined within its own technical vocabulary relating to forms and phenomena not otherwise described. In the first place, the ecologist must have at his command, and be able to use with precision at least part of the vocabulary of many other sciences. Secondly, many of the terms descriptive of the natural background are words of common speech which may or may not have a clearly delimited meaning, and may lately have suffered technical restriction. The translation of these words into cumbrous Greek and Latin derivatives, which has been the expressed policy of some ecologists, seems in the present state of knowledge merely to add to the synonymy without advancing clarity of expression.

In dealing with most of the technical terms and words of which the common meaning has been restricted, Mr Carpenter has followed the principle of quoting either the meaning attached by the author first using the word or that adopted in a more readily available work, and in each case of giving a reference to the publication. This method has great advantages; but in a rapidly growing science the meaning that becomes more generally adopted may differ from that first proposed, and the recording without comment of several meanings under the same term does not provide a guide to current usage.

Mr Carpenter has, properly, cast his net widely, and the number of synonyms, overlapping terms, and words of ill-defined meaning is remarkable. If the work had no other merits it would have value in bringing into sharp focus the real difficulties that face the research worker who seeks the unequivocal presentation of his results, and the pressing need for ecologists to put their terminological house in order.

C. DIVER.

AN ECOLOGICAL PANORAMA

W. C. Allee & Karl P. Schmidt (1937). Authorized and rewritten edition of **Richard Hesse's** *Ecological Animal Geography* (*Tiergeographie auf ökologischer Grundlage*). 597 pp., many illustrations. John Wiley and Sons Inc., 440 4th Avenue, New York; and Chapman and Hall Ltd., 11 Henrietta Street, Covent Garden, London, W.C. 2. Price £1. 10*s*.

"The principal impulse by which I was directed", wrote Baron Von Humboldt from Potsdam in 1844, "was the earnest endeavour to comprehend the phenomena of physical objects in their general connection, and to represent nature as one great whole, moved and animated by internal forces.... I would therefore venture to hope that an attempt to delineate nature in all its vivid animation and exalted grandeur, and to trace the *stable* amid the vacillating, ever-recurring alternation of physical metamorphoses, will not be wholly disregarded even at a future age." Although no one else has attempted to paint on such a vast canvas as that covered by Humboldt's *Cosmos*, we are coming again into an age when the task of general correlation, the drawing of provisional patterns and the creation of working frameworks that can give scale and proportion to individual surveys by explorers, naturalists and ecologists, is once more becoming respectable, and less liable than it was to the accusation of superficiality in execution, and impatience to reach easy conclusions which will provide satisfactory fodder for University teaching. There have been several attempts in recent years to describe the ecological structure of the animal world against its natural background of vegetation and physical forces. Among these may be mentioned: in German, Dahl's *Ökologische Tiergeographie*; in English, Newbigin's *Plant and Animal Geography*; and in Russian, Heptner's *General Zoogeography*. Hesse's book is perhaps best known, since, in

spite of certain drawbacks, it is in many ways the best-balanced and most comprehensive in its scope. Realizing its value, the two American editors set out to revise and bring it up to date.

It would have been better if they had been content only to translate and add some notes, or else to write an entirely new book with their own ideas in it. For they state that passages with which they disagreed have been intentionally omitted or changed, and the result is that the reader coming fresh to this edition can seldom know, though he can sometimes guess, which is Hesse, and which is Allee or Schmidt. One is reminded somewhat of the old jest about a Limited Company, that it has no body to be kicked and no soul to be damned.

Any reviewer who takes his task seriously must be in a certain difficulty in trying to assess the true value of the book, for in dealing with such a vast field as the authors do they must be expected to have covered the ground unequally. Similarly, the reviewer has to judge rather by the limited sections of the subject that are familiar to him, how far the text is a fair mirror of modern research on ecological animal geography. For instance, the chapter on Polar Regions is notable in containing no references at all to any field surveys done by European expeditions since the War. Yet the results of these dozen or so expeditions that have carried out work on animal ecology have given a very clear picture of the structure of these arctic and subarctic communities, and the results have mostly been published in official British journals of ecology, and (less accessibly) in Scandinavian and Russian expedition results. When one is told that the "purple sandpiper, *Erolia maritima*, of Spitzbergen, has accustomed itself to a plant diet" (which is absurd, as it lives on insects and Crustacea) how much are we to rely upon other facts cited in regions of knowledge of which we know nothing?

It is no excuse for a book which sets out to cover a very large field to say that mistakes are inevitable on account of the largeness of the field. We expect, rather, that an authoritative book will be thoroughly learned and complete. In the present instance, it was obviously impossible for any two authors to cover effectively the whole field without constantly getting out of date before they could master it and write it up. Yet a more organized attempt by many authors would have lacked the coherence which is achieved in many of the chapters.

Turning to more constructive criticism, let us consider the scope of the book, and the range of information and ideas that a student at the University would be likely to acquire from it, that he could not easily acquire by other means. There is a clear distinction made between the kind of ecological animal geography intended in the present treatment, and the type of historical problem that is bound up with long-continued evolution and migration, and the changing major barriers to dispersal, such as sea and land, mountain and desert. A special chapter explains this point and gives examples of discontinuous range and evidence of former extension and movements. The authors are unable to refer to any convenient text-book on this historical aspect, for none exists.

Other early chapters deal with the general limits to animal distribution, illustrated by examples. Although there are a good many rather meaningless sentences, such as "animal life is not tied hard and fast to unalterable values of the conditioning factors", the discussion is well-sustained, interesting especially in making a bridge between ordinary field ecological facts and physiological knowledge, and is easy to read and follow. No one could read this part of the book without finding much information he was quite unaware of, and getting some sense of the drift of American ideas in this phase of ecology.

The major part of the book is concerned with the three great sections of animal habitats and their faunas: marine, fresh-water, and land. Most of the facts that are cited are backed by references at the end of each chapter, and the easy traps which many European ecologists have fallen into in assuming adaptive values for structures and habits, are skilfully avoided; the authors mention in their introduction that in this respect they have differed a good deal from Hesse in their interpretations and objective approach. It is impossible to follow all the sections in detail, but it may be said freely that the whole of it makes interesting, often fascinating reading, and were it not for a lurking suspicion that a good deal of the detail has not been checked back to the original sources, and the fact that the literature is not up to date, one would acclaim it as a worthy follower in the tradition of Humboldt's *Views of Nature*, though not up to the standard of his *Cosmos*.

The student who reads this book will learn of the existence of innumerable curious facts of which he had previously no inkling, and he will never again with any justice be able to ask a harassed supervisor to find him an ecological problem on which he can do research. This book offers him a good many thousand. Would he like to study the effect of surf action on marine molluscs, the food of sand-dwelling worms, the locomotion of plankton, why flounders do not become sexually mature in fresh water, the habits of animals that live in moss, the ecological uses of fat, the influence of snakes on other animals, the occurrence of the burrowing habit, why grasshoppers favour grassland, the occurrence of alpine beetles, or the fauna of caves, or what? Perhaps in stimulating the ecologists to study and clarify all these smaller problems in their larger setting, the authors of this book will have fully compensated for any mistakes or omissions they may have made. I know of no other means of approaching this huge field of information through any book in the English language, and shall certainly draw upon it for many purposes for many years. To an alert reader, the book is worth its high price.

CHARLES ELTON.

HERD AND FLOCK

(1) F. Fraser Darling (1937). *A herd of red deer.* 215 pp., 8 plates, 10 text-figures and 4 maps. Oxford University Press. Price 15*s*.

(2) F. Fraser Darling (1938). *Bird flocks and the breeding cycle.* 124 small pp., 1 photo and 1 text-figure. Cambridge University Press. Price 6*s*.

(1) In the north-west of Scotland lies some of the wildest hill country in the British Isles. On one part of this, an area of 52,000 acres on which about 1300 red deer (*Cervus elaphus*) live almost unmolested, the author spent two years studying the habits and territory and population inter-relations of the deer. He brought to this pioneer investigation a serious purpose borne of a scientific training, and experience in the Imperial Bureau of Animal Genetics in Edinburgh, together with the complete freedom to carry out his research plans that a Leverhulme Research Fellowship afforded. Watching deer at all is a difficult pastime, but to follow them constantly for two years and get to know every bit of the eighty square miles where they live, and the movements and habits of each group of animals, to recognize the different ages and even individuals, and to become sufficiently invisible and unsmellable to see them behaving naturally, requires a tremendous amount of prolonged stalking and waiting, and facility akin to that of the professional deer-stalker who has been brought up to this life. And yet, withal, it is necessary to retain scientific and critical judgement and not to get out of touch entirely with the stream of ecological thought. The following remark is interesting in this connexion: "If you are to develop this quality of sight so that deer and other objects stand out from the hill in your field of vision, not much reading should be undertaken. This seems to alter focal habit, and a hill-side, instead of having depth, becomes merely a flat homogeneous expanse."

The country is described, and then the author's technique and personal reactions to field work. We learn, for instance, that he went barefoot in the summer and thereby greatly increased the awareness of all his senses.

The environment of the deer is described: climate, ground vegetation, the shape of the country, the insect enemies and the parasites of the deer. But, as with all social animals, it is the other deer which form a dominant part of the environment to any individual, and this part of the story occupies most of the book. The style is easy and gives one a real feeling of the country and of the "outlook" of the deer themselves. There is, in addition to scientific enthusiasm and critical judgement, a strong element of aesthetic enjoyment running through, as well as a spontaneous sympathy with wild animals and a desire to communicate this to others.

Fraser Darling finds the social system of red deer to be a matriarchy, with the sexes running in separate herds for most of the year. He mapped the distribution of groups and

their territories, and followed the changes in social and sexual organization through the seasons. The physiological and psychological discussion of these facts must be left to others; but certain very interesting ecological facts also came out of the investigation. It is often assumed that deer in Scotland are kept down by deliberate controlled shooting. In many places the stags are of course shot in some numbers, and the hinds also are thinned out to some extent as a measure of management. But it is very surprising to find how small the biotic potential of the species really is, after allowance has been made for "infant mortality", mortality before breeding, non-breeding females, and so on. The most astonishing thing of all is the evidence that something like 50% of calves are killed during the first five days after birth, when they are temporarily deserted by the mother and are attacked by predators, especially foxes. In other words, a game warden seeking to prevent deer from over-increasing on a national park in Scotland, would find it simplest to encourage foxes. A very similar condition has been claimed by Peter Frechen for the caribou on Melville Peninsula, in Arctic Canada, where he says arctic foxes destroy the young during the first few days after birth. It is most remarkable that half each new generation should be destroyed within five days, in a species such as the red deer, which may live twenty years, and commonly half that much. The whole question seems worthy of a special study, in view of the very marked increase of deer that is taking place now in many parts of the British Isles.

The author lets his observations mostly speak for themselves. The only weak point in the field work seems to be the difficulty of identifying individuals of different classes at a distance. Here the worker has simply to rely on training and practice. There is no rigid proof. And yet it is on this power of distinguishing, and even of recognizing individual deer, that much of the finer observation is built. But the point is honestly met and discussed, and it can be said that without any doubt Fraser Darling has set a new standard for field study of large mammals, a standard which one would like to see extended to African big game and to the ecological-physiological-psychological study of wild mammals generally.

CHARLES ELTON.

(2) There are many things in this book that will come as a relief to the ornithologist in particular. It is, though it should not be, unusual for a book to be written about birds which treats them as subjects for zoological research. In this case it is especially interesting that the thesis is based wholly upon field work, though of course this sets definite limitations to the degree to which many statements are supported or even verifiable. However, even if the author is prone to throw out ideas, constituting a challenge to the laboratory worker to confirm or disprove his conjectures, we can nevertheless be thankful for the stimulation provided. An instance that occurs is the suggestion on page 7 that the cere may function as a photoreceptor conveying impulses that stimulate the pituitary to active secretion. This is the sort of suggestion that is apt to be quoted by subsequent authors as a definite statement, and so the sooner the presence of nerve endings is demonstrated in the cere, the better. Dr Fraser Darling has provided plenty of hard work as well as food for thought.

The first chapter contains a brief recapitulation of what is known about sexual periodicity and the factors which control it, with particular reference to birds. This might perhaps have been a little longer and a little more critical, but the main points, that light and activity have in certain cases been proved to have a connexion with the increase of gonad size, are brought out, and climatic conditions in the north-west of Scotland reviewed in this light.

Chapters 2 and 3 are the most valuable part of the book. The detailed description of the arrival and gradual assumption of the breeding frame of mind, of two species of British gulls, the herring gull (*Larus a. argentatus*), and the lesser black-backed gull (*Larus fuscus affinis*) provide a model for many field observers inasmuch as the main contentions are kept clear and irrelevant details are excluded. The correlation demonstrated between early laying dates, larger clutches and strength of the breeding colony goes a long way to support the author's main argument, which is that in social birds the visual and auditory stimuli provided by the surrounding colony effect an acceleration in the onset of breeding condition. At present both the physiological mechanism to which he refers such phenomena and the observations themselves need verification, but a fruitful field is certainly provided for further research.

It should be remembered that the author is only concerned with the factors which lead to ovulation; the question of how much courtship actions are concerned only with successful fertilization is not discussed. While commending the author for adherence to the main argument, one feels that it would have been interesting to hear how much courtship persisted into the later breeding phases.

The fourth chapter contains brief references to other species in which similar principles may hold good, and indicates many lines that may profitably be followed. It is to be hoped that such an excellent lead as has been given to us in this book will not be neglected either in the field or the laboratory.

H. N. SOUTHERN.

THREE HUNDRED YEARS OF CONSERVATION

C. L. Collenette (1937). *A history of Richmond Park: with an account of its birds and animals.* 164 pp., 5 plates and 1 map. Sidgwick and Jackson Ltd., 44 Museum Street, London, W.C. 1. Price 7*s.* 6*d.*

The planning of national parks is much in people's minds, but we do not hear a great deal about the possibilities of preserving and managing the plant and animal populations of the national parks that have been proposed for this country. A book which gives glimpses of how this has been done in a more or less carefully managed park near London is therefore interesting, even though it deals with a comparatively small area.

One of the difficulties of applying ecology to the successful deliberate balancing of different elements in a national park, will be that game management and conservation have in Great Britain become a body of traditional lore, long before they had a chance to be a science. That is why countries with a shorter history of large-scale wild life management, such as the United States and the U.S.S.R., are so enormously ahead of us in its scientific application. In these remarks, it is of course assumed that such a thing as the management of populations of wild plants and animals is a practical possibility. The policy of letting everything rip, without control, is only possible in very large areas such as the Kruger National Park in South Africa, which can form a little kingdom of wild country chiefly dedicated to faunal preservation.

A few years before his execution, King Charles I resolved to make himself a fine deer park near London. This project he carried out regardless of the opposition of his advisers, and of all those people who owned rights and private property on what is now Richmond Park. This ground, a mixture of waste land, common, and Crown Land, mostly covered with gorse and oakwoods, among which were certain private houses and properties, had long been hunted in by English kings. In the time of Henry VIII it was known as Sheene Chase. After long negotiations, the owners were bought out (rather handsomely), a wall was built, and in 1637 the New Park came into existence, with rangers to supervise the deer. The king had a little hunting, in fact he still hunted there while he was prisoner, before his death.

During the Commonwealth, the Park passed into the hands of the City Aldermen, whose management did not go much beyond an attempt, frustrated by Parliament, to cut down and sell the oaks, and the consumption of venison at City banquets. With the return of Charles II, the Park went back to Royal patronage, under which it was administered by various rangers until 1904, when it came under the control of the Commissioners of Works. During all this time two kinds of deer were kept and more or less carefully managed and protected. The number of fallow deer (*Cervus dama*) was large, varying from about 1300 to 2000 on an acreage of about 2300; red deer (*C. elaphus*) were fewer: from 50 to 200. Since 1904 small game has no longer been preserved for sport; but the deer, reduced now to about 300 and 80 respectively, are still kept and have an important influence on the vegetation, by eating down the seedlings of young trees. From being a more or less private park for the aristocracy to hunt in (the deer were still hunted in the early nineteenth century), the place has become a public resort in which the policy is to encourage most wild birds and animals indiscriminately.

The three dominant factors which have caused changes in the park are the hunting motive, giving place to a wider conservation; the amount of public access; and the inter-relations of

animal life to the vegetation. There are some curious points unearthed by the author's patient research into archives, and his field knowledge of the park conditions and life. The deer population fluctuated somewhat, but most of the time seems to have kept a very high level without harm. The herds were added to from time to time, were often fed in winter, and in the early days the oaks are thought to have been pollarded to give browse to the deer in times of scarcity. Protection was stringent, and no doubt enemies, such as foxes, were discouraged. The only recorded epidemic was in 1886–7. As a result of this high density, the deer have kept the area comparatively open, while neighbouring commons are grown with scrub.

Rabbits must have aided this seedling tree destruction, for in 1904 when the Government took over management, 2400 rabbits were destroyed. After this relief from rabbit pressure it was noticed that many young birches began to grow up. In 1934 some New Forest ponies were introduced, and are breeding successfully. However, there are a good many plantations that the deer and ponies cannot enter. Deer also destroyed reeds introduced for the water-fowl, and part of each of the two larger ponds is now separated as a bird sanctuary.

A curious incident was the introduction of wild turkeys probably in the reign of George I. There were as many as 3000 of these birds, which ate the acorns, were also artificially fed, and afforded royal sport when they were chased by dogs and treed and shot. This turkey population died out during the nineteenth century. The swan is now regarded as a pest through its attacks on other water-fowl, although it is swans that give the earliest record of game management in the British Isles. A molecatcher was kept to prevent horse-riders from having accidents.

The history of access is given: a brewer called John Lewis fought and won a test case, after which the public was admitted for the first time in fairly large numbers (1758), but only over ladders on the walls, so that the deer should not get out. From the early nineteenth century onwards some domestic animals were also kept in the Park. One result of excessive human visitors is the beating down of dead bracken in which certain birds make their nesting sites. The pollution of Beverley Brook has mostly stopped the fine annual run of young eels to the ponds that used to be observed. But the ponds themselves contain various other fish.

The first part of the book has most of the historical material. Part 2 is given up to the fauna, chiefly birds, for which many valuable records are made under the various species. One of the modern problems is evidently what should be classed as vermin. Foxes persist in spite of killing (116 were destroyed in six years), there are five badger earths, the grey squirrel is permanent, although 200 were shot in five years. And a small population of pheasants and partridges hangs on without any special assistance. There must be innumerable questions that could be studied by ecologists in Richmond Park, and that would throw light on the inter-relations of the 80 regular resident or visiting birds, the dozen or so mammals, not to speak of the thousands of other animal species. It is to be hoped that this monograph will give a useful frame into which further studies can be fitted. Still more one wishes that the future large national parks should have faunal surveys done now before they are handed over to regional committees armed with extraordinary powers.

CHARLES ELTON.

IMPROVED PHENOLOGY

H. C. Gunton (1938). *Nature study above and below the surface: a bridge between amateur and professional.* With a preface by C. B. Williams. 134 pp., 18 text-figures and photos. H. F. and G. Witherby Ltd., 326 High Holborn, London, W.C. 1. Price 7*s*. 6*d*.

This book will be very useful to ecologists because it gives such an excellent account of modern methods of compiling phenological records, together with an analytical discussion of the results, illustrated with numerous diagrams and tables. Much of it is chiefly entomo-

logical in scope but the subject is well covered and includes mention of most recent researches of interest to field naturalists. An important feature is the way in which the book suggests useful lines of work for the amateur and stresses the need for collaboration.

The book is well produced and generally accurate although it contains a few misprints (e.g. p. 31, *phlaes* for *phlaeas*, Nymphauds for Nymphalids, *paleacia* for *paleacea*) and several misleading statements (e.g. p. 29, "many moths, as well as butterflies, are attracted to blossoms, and feast on their pollen"). These are, however, but small blemishes and the book should be well received.

B. M. HOBBY.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology,* Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts are issued free with the *Journal*. They can also be obtained separately in stiff covers, printed on one side of the page to allow them to be cut out for pasting on index cards, by non-subscribers, from the Cambridge University Press, Bentley House, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free, (about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, F. C. Evans and B. M. Hobby.

1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) Marine and brackish

See also **155, 185, 288**

143. Moore, H. B. and others (1937). "Marine fauna of the Isle of Man." (Reprinted from Proc. Liverpool Biol. Soc.) University Press of Liverpool, 175 Brownlow Hill, Liverpool. Price 2*s*. (2*s*. 6*d*. post free). 293 pp. and 3 charts.

Lists of all invertebrates and fishes known to have been found within a radius of 5 miles from the shore of the island. Including bibliography. Notes on seasonal occurrence, depth and type of habitat are incomplete. Some short lists of species characteristic of different habitats are given. (See also **288**.)

144. Wells, A. Laurence (1938). "Some notes on the plankton of the Thames Estuary." J. Anim. Ecol. 7: 105–24.

Collections of phyto- and zooplankton (mostly at Southend-on-Sea) were made between November 1933 and April 1937. The results are described against the general background of Thames Estuary sea-food industries, which include cockle, oyster, whitebait, and shrimp, all depending mainly upon plankton for their basic resource. Special account is given of seasonal variation in the diatom and Copepod community, and to quantitative changes with the tidal cycle. The methods of sampling are described, many useful ecological notes are given on various groups studied, and two useful charts showing the general distribution of types of sea-bottom and important animals within the Estuary.

145. Raitt, D. S. (1937). "The benthic Amphipoda of the north-western North Sea and adjacent waters." Proc. Roy. Soc. Edinburgh, 57: 241–54.

This order is an important element in the food of marine fish. Analysis was done (*a*) of bottom sampler material taken between 1922 and 1930 (of which a distribution map is given for the numbers of samples), which yielded 1605 specimens of Amphipods, of 79 species; (*b*) 69 haddock stomachs, of which 42 contained Amphipods: 1599 specimens and 47 species. The average frequency of specimens of this order in bottom samples was about 540 per 100 sq. m. for the Coastal zone, 400 for the Offshore zone, and 180 for the North-eastern zone. A complete list of species and their general distribution in the area is given, and remarks on the species composition in different zones. *Ampelisca* (of which eight species were taken) formed the commonest type: 55% of specimens in the grab samples, and 45% in the haddock stomachs. The survey therefore establishes *Ampelisca* as one of the key-industry animals in bottom-feeding fish production, more particularly affecting post-larval and adolescent fish.

146. Forrest, J. E. (1938). "Notes concerning some animals obtained from three German warships recently salved at Scapa Flow, Orkney." Scot. Nat.: 3–8.

These vessels were sunk in 17 fathoms of water, where they remained for 16 years. The fairly extensive list of species includes only those which remained after the vessels had been scraped, but nevertheless seems to indicate a great variety of marine life in the seas around the Orkneys.

147. McMillan, N. F. (1937). "Marine Mollusca at Belan Fort, Foryd Bay, Caernarvonshire." North Western Nat. 12: 401–2.

A list of species from one small area.

148. Fisher, N. (1937). "Nudibranchs from N.E. Ireland." Irish Nat. J. 6: 200–2.

List of sea-slugs with good habitat notes.

149. Lynn, M. J. (1936). "The scarcity of *Zostera marina* (slitch, eel-grass or grass-wrack) in Strangford Lough." Irish Nat. J. 6: 107–17.

Describes the diminution of *Zostera* locally, with a general account of the decrease of the plant elsewhere. Causes of decrease are analysed: no single one can be given sole responsibility.

(*b*) Freshwater

See also **160, 161, 162, 164, 178, 186, 188, 192, 196, 197, 283, 287**

150. Macan, T. T. (1938). "Evolution of aquatic habitats with special reference to the distribution of Corixidae." J. Anim. Ecol. 7: 1–19.

Survey of all species of lesser water-boatmen found in the English Lake District. Species classified into groups according to their habitat, and position of this habitat in the succession series from low to high organic content of soil previously worked out by Pearsall. There is a special group in high tarns.

151. Wilson, G. (1937). "Notes on mosquitoes of Belfast." Irish Nat. J. 6: 166–7.

Eight species, with some habitat notes.

152. Kimmins, D. E. (1938). "British Ephemeroptera, Plecoptera and Trichoptera in 1936." J. Soc. Brit. Ent. 1: 202–9.

A valuable addition to knowledge of the distribution of these Orders.

153. Cowley, J. (1938). "Notes on British Odonata in 1937." Entomologist, 71: 108–10.

Dates of occurrence in Surrey and Sussex.

154. Hammond, C. O. (1938). "The dragonflies of Byfleet." Entomologist, 71: 84–6.

Habitat notes of 23 species.

155. Reid, D. M. (1938). "Forms of *Gammarus* from Ireland." Nature, 141: 690.

G. duebeni, usually a brackish-water species, was found generally distributed throughout Ireland in rivers and freshwater loughs, in waters of widely varying *p*H. *G. pulex* was reported only from Lough Erne.

156. Smith, S. H. (1937). "Distribution of the crayfish (*Astacus pallipes*)." Naturalist, 17.

Notes on Yorkshire localities.

157. Fry, A. H. (1938). "The upper Avon and its water meadows." Avon Biological Research, Annual Rep. 1936–37, 20–8.

Describes the course of the river through different geological formations and soils, and gives a classification (with map based on Land Utilization Survey) of various pasture types in the Avon above Salisbury. The subject has a relation to fisheries through silting and food supply and water.

(c) Land

See also **153, 154, 200, 210, 233, 283**

160. (London Natural History Society) (1938). "The survey of Limpsfield Common." London Nat. for 1937: 46–66.

Preliminary studies of the ecology of a Surrey common, organized by a committee of the Society, with the help of various workers. The main vegetation types have been mapped and soil acidities determined. Lists of species include bryophytes, fungi, lichens, plant galls, Diptera, Amphibia, reptiles, birds and mammals. Careful habitat notes are given for the species. "The survey of Limpsfield Common aims at a knowledge, as complete as possible, of the fauna and flora of the area, its numbers of individuals, their fluctuations and the causes, their interrelations, and their habits as influenced by the area and its conditions. The basis of such a study must be correctly identified plants and animals to enable past, present and future knowledge to be correlated."

161. Fitter, R. S. R. (1938). "Mammal, etc., recording in 1937." London Nat. for 1937: 92–3.

A list of 42 mammals, five reptiles, and six Amphibia, recorded within 20 miles of the centre of London since 1900. Most of them (except for many of the bats) have been found also since 1920.

162. Homes, R. C. (ed. by) (1938). "Birds in the London Area, 1937. Report on bird-life within twenty miles of St Paul's Cathedral." London Bird Report for 1937: Suppl. to London Nat. pp. 1–34.

Besides the usual type of list with local records of occurrence, there are special notes upon certain species: magpie, which avoids densely populated areas; red-backed shrike, with a scattered distribution which is discussed; coot, of which large flocks come into the area from outside in the autumn; pied wagtail, which had a roost of sometimes over a hundred birds in Richmond Park. A complete census of coots, great-crested grebes, and all species of ducks was done on 18 December 1937, on a number of the main pieces of water round London. There are also notes on migrants and upon ringing work.

163. Tully, H. (1938). "Some birds on the north Northumberland coast in June and July, 1937." Vasculum, 24: 40–5.

Compares observations with those recorded in works by Chapman (1907) and Bolam (1912), and suggests that there may have been changes in the habits of several Northumberland species.

164. Frank, A. Stanley, Flintoff, R. J., Green, J. & Patterson, J. (1937). "Notes on the Hole of Horcum, Saltersgate, North Yorkshire. 3. The birds of the District." North Western Nat. 12: 125–40.

The birds are listed under general habitats (woods, moorland, heaths, marsh, etc.) instead of in systematic order, and good habitat records are given for each, with seasonal variations.

165. Steel, W. O. (1938). "Insect life in a dying willow." London Nat. for 1937: 68–9.

Notes on eleven species, in wood and under bark.

166. Hayhurst, H. (1937). "Insect infestation of stored products." Ann. Appl. Biol. 23: 797–807.

A survey of insects found on the London, Midland and Scottish Railway.

167. Wilson, G. Fox (1938). "Pests of commercial ornamental plants." Scientific Horticulture, 6: 102–16.

The chief forms dealt with are: stem or bulb eelworm (*Anguillulina dipsaci*), already recorded from over 300 species of plants; fern or leaf eelworm (*Aphelenchoides olesistus*) causing leaf infection of ferns, also of many other plants; Tarsonemid mites, on the under-sides of leaves of various species; rhododendron bug (*Leptobyrsa rhododendri*); glasshouse leaf-hopper (*Erythroneura pallidifrons*) sucking under-sides of leaves; rhododendron white fly (*Dialeurodes chittendeni*), whose honey-dew on upper leaf surfaces encourages certain moulds; knapweed aphis (*Macrosiphum jaceae*), on cornflowers (*Centaurea*); tulip aphis (*Anuraphis tulipae*), attacking bulbs of iris and tulip, and corms of *Gladiolus*; scale insects and mealy bugs in a large number of plants; rosy rustic moth (*Hydroecia micacea*), a stem miner of wild plants, sometimes attacking *Antirrhinum* and *Dahlia*; swift moths (*Hepialus*), attacking roots of many species; carnation tortrix moth (*Tortrix pronubana*), leaf-rolling and bud-eating larvae, polyphagous; vine weevil (*Otiorrhynchus sulcatus*), larvae on roots, etc., and adults nocturnal on leaves of various kinds of plants; violet midge (*Dasyneura affinis*), leaf-rolling; fruit flies on *Berberis*, *Cotoneaster*, *Pyracantha* and *Rosa*. The need for constant vigilance is stressed, as the polyphagous habits of many pests enable them to change from wild plant hosts to cultivated ones. Methods of control for different pests are given, and an appendix lists the chief plant hosts and their known pests.

168. Guichard, K. M. (1938). "Aculeates on the Norfolk coast." London Nat. for 1937: 71–2.

27 species of bees and wasps listed from *Psamma* sand dunes.

169. Faris, R. C. (1936). "Records of some bees, wasps, and ants from County Cavan, in 1933." Irish Nat. J. 6: 143–5.

Includes some ecological notes.

170. Niblett, M. (1937). "Some observations on plant-galls caused by gall-wasps (Cynipidae)." Proc. S. Lond. Ent. Nat. Hist. Soc.: 61–8.

An account of abundance, host-plants and galls, chiefly from observations made in Surrey.

171. Donisthorpe, H. St J. K. (1938). "A preliminary list of the Coleoptera of Windsor Forest." Ent. Mon. Mag. 74: 21–7, 67–77, 115–26.

172. Kaufmann, R. R. U. (1937). "Investigations on beetles associated with carrion in Pannal Ash, near Harrogate. II and III." Ent. Mon. Mag. 73: 227–33 and 268–72.

173. Stelfox, A. W. (1937). "Notes on the distribution in Ireland of the long-horn beetles, *Strangalia aurulenta, S. quadrifasciata* and *S. armata*." Irish Nat. J. 6: 156–8.

Armata has the widest distribution, while the other two are confined to the southern and south-eastern counties. The three species are illustrated.

174. Fordham, W. J. (1937). "Mole's nest beetles in East Yorkshire." Naturalist: 265–7.

Analysis of the beetle fauna of over 100 mole nests examined between 1913 and 1922.

175. Stanley-Smith, F. (1937). "*Cosmia* (*Xanthia, Mellinia*) *ocellaris*, Brkh." Proc. S. Lond. Ent. Nat. Hist. Soc.: 73–9.

A useful contribution to the knowledge of the life-history of this rare moth. The larvae feed in the catkins of poplar which they probably desert later in order to bore into the high leaf buds.

176. Klimesch, J. (translation by **Jacobs, S. N. A.**) **(1937).** "Some remarks on the genus *Nepticula*, Z." Proc. S. Lond. Ent. Nat. Hist. Soc.: 92–107.

An account of the biology of these minute leaf-mining moths, with notes on collecting, breeding and mounting.

177. Otter, G. W. (1938). "On the morphology of the larvae of three species of Cecidomyidae (Diptera) from knapweed (*Centaurea*) flowers." Trans. R. Ent. Soc. Lond. 87: 39–68.

The species described (*Lestodiplosis miki, Clinodiplosis cilicrus* and *Dasyneura miki*) play a comparatively small part in the economy of the insect population in the flowers of *Centaurea nigra*.

178. Oldroyd, H., Parmenter, L. & Pugh, C. H. Wallace (1938). "Dolichopodidae (Dipt.) from Silchester Common (Berks.)." J. Soc. Brit. Ent. 1: 232–3.

27 species were obtained along the banks of a stream, mainly in boggy places. The most abundant species were *Dolichopus popularis, Hercostomus nigripennis* and *Gymnopternus aerosus*.

179. Thomas, I. (1938). "On the bionomics and structure of some dipterous larvae infesting cereals and grasses. III. *Geomyza* (*Balioptera*) *tripunctata* Fall." Ann. Appl. Biol. 25: 181–96.

Cereals and grasses were preferred in the following order: (1) *Lolium perenne*, (2) *L. italicum*, (3) wheat, (4) barley, *Poa trivialis, Dactylis glomerata*, (5) *Cynosurus cristatus*, oats, (6) *Festuca rubra*. Three parasites were bred: *Phaenocarpa livida, Chasmodon apterous* and *Stenomalus* sp.

180. Harrison, G. Heslop (1936). "The Psyllidae, or jumping plant-lice, of Northumberland and Durham." Trans. Northern Nat. Union, 1: 217–28.

List of species with good habitat notes, including host plants, and indication of distribution of the species abroad. It was found that a great many species remain on their host plant during winter, sheltering at its base and on the lower twigs.

181. Harrison, G. Heslop (1938). "Observations on the British Psyllidae. II. Notes on the *Salix*-feeding Psyllidae." Ent. Mon. Mag. 74: 8–11.

Mainly host-plant range.

182. Dallas, J. E. S. (1938). "*Atypus affinis* Eichw. in the London District." London Nat. for 1937: 24–5.

Distribution of this trap-door spider in sandy heaths round London (it was found exceptionally on chalk grassland). It is thought that increased trampling by people is destroying its colonies.

183. Waterson, A. R. & Quick, H. E. (1937). "*Geonemertes dendyi*, a land Nemertean, in Wales." Proc. Roy. Soc. Edinburgh, 57: 379–84.

This is apparently the first record of a land Nemertean worm established in the temperate climate of Europe. Internal and external characters are described. The worms are active at night, and are found in damp shady places near streams or trees. Eggs were found in March, but were laid in captivity in October, November and April. Previously known from West Australia, and a glasshouse in Germany, it has now been found around Swansea, associated with land planarians (*Rhynchodemus terrestris*) and a list of Mollusca which is given. It has been found in the same area in three successive years.

(*d*) Small islands

184. Warwick, T. (1938). "Notes on mammals of the isles of Barra, Mingulay, and Berneray, Outer Hebrides." Scot. Nat.: 57–9.

Notes on two aquatic and five land mammals. Most of the notes are on *Apodemus hebridensis* (collected on Barra and Berneray, and said to occur on Mingulay). Other species noted on land were *Sorex minutus*, *Rattus norvegicus*, *Mus musculus* (living wild), and rabbits.

185. Southern, H. N. (1938). "A survey of the vertebrate fauna of the Isle of May (Firth of Forth)." J. Anim. Ecol. 7: 144–54.

The first part of this paper describes the occurrence, dimensions (including weights) and parasites of the house mouse (*Mus musculus*) living out of doors. The second part gives counts of the breeding pairs of land, shore, cliff and ternery, and predatory birds, with a general description of the island and a map showing vegetation zones. There are also some notes on non-breeding birds. There have been changes in numbers in several species in recent years. The most striking is in the herring gull (*Larus argentatus*), from 58 pairs in 1924 to 455 in 1936 (the date of the census given here).

186. Harrison, J. W. Heslop & Peacock, A. D. (ed. by) (1938). "The natural history of the Island of Raasay and of the adjacent Isles of South Rona, Scalpay, Longay and Fladday." Scot. Nat. (for pages see below. Earlier parts noticed in J. Anim. Ecol. (1938) 7: 167–8, No. **38**).

"VIII. Notes on the bird life of the island of Raasay, Inner Hebrides." By **G. W. Temperley.** Pp. 11–27.

The history of the island has greatly affected the bird life. Before 1852 the Macleods who owned it maintained a large amount of natural game, and the island was densely populated by people. After 1852 a new order evicted 94 families in order to make the island into a sheep ranch, and it reverted to rough grazings. Eventually it passed into a regime of intensive game preservation, with the introduction of partridge and pheasant and destruction of enemies of game birds (e.g. hen-harrier, peregrine, merlin, rook, heron) and new plantations were made. After 1912 the island was used for ironstone mines and game preservation declined. After the War the mines were closed and the island passed into the hands of the Board of Agriculture for Scotland. During the post-1912 period game-birds and animals decreased greatly, and deer and grouse are now very scarce, but crows are abundant. A full list of birds is given, with habitat notes and general indications of numbers and breeding status.

"IX. The Ephemeroptera, Plecoptera, Megaloptera, Neuroptera and Mecoptera of Raasay and the adjacent islands of South Rona, Scalpay, and Pabbay." By **J. W. Heslop Harrison.** Pp. 28–30.

30 species recorded, with some general habitat notes for some of them.

"X. The aquatic Coleoptera of Raasay and of the adjacent islands of South Rona, Fladday, Scalpay, Longay, and Pabbay." By **G. Heslop Harrison.** Pp. 60–4.

42 species of water beetles recorded (43 have been recorded by another worker for Skye). General habitat notes and locations are given for some species. *Aulonogyrus striatus*, a Gyrinid new to the British Isles, and usually considered a Mediterranean species, was taken on Raasay in a low-lying loch.

187. Harrison, J. W. Heslop (1937). "The Lepidoptera of the Isle of Raasay and of the adjacent islands of Scalpay, South Rona, Fladday, and Longay." Proc. Univ. Durham Phil. Soc. 9: 305–28.

Results of field expeditions in 1934–36 to these islands of the Inner Hebrides. 329 species were collected, and a certain amount of habitat information is recorded.

188. Harrison, J. W. Heslop (1937). "The Trichoptera of the Isle of Raasay and of the adjacent islands of South Rona and Scalpay." Proc. Unvi. Durham Phil. Soc. 9: 329–31.

45 species, with localities and a few habitat notes.

189. Harrison, J. W. Heslop (1937). "The Cecidomyidae or gall gnats of the Isle of Raasay and of the adjacent islands of Scalpay, Rona, and Longay." Proc. Univ. Durham Phil. Soc. 9: 332–5.

46 names recorded, with host plants.

190. Harrison, J. W. Heslop (1937). "The Hymenoptera of the Isle of Raasay and of the adjacent islands of Scalpay, South Rona, Fladday, and Longay." Proc. Univ. Durham Phil. Soc. 9: 336–40.

20 bees, five ants, ten wasps, one Chrysid, four Ichneumonids, 13 Cynipids, four sawflies.

191. Harrison, G. Heslop (1937). "The Psyllidae or jumping plant-lice of Raasay and of the adjacent islands of Rona, Fladday, Scalpay, Longay, and Fladday." Proc. Univ. Durham Phil. Soc. 9: 341–4.

Four summers' collecting produced 32 species, for which good host-plant and habitat records are given.

192. Harrison, J. W. Heslop (1937). "The Hemiptera-Heteroptera of Raasay and of the adjacent islands of South Rona and Scalpay." Proc. Univ. Durham Phil. Soc. 9: 346–51.

76 species with some general habitat notes.

193. Harrison, J. W. Heslop (1938). "The Rhopalocera of the islands of Coll, Canna, Sanday, Rhum, Eigg, Soay, and Pabbay (Inner Hebrides), and of Barra, Mingulay and Berneray (Outer Hebrides)." Entomologist, 71: 18–20.

Records of sixteen species. Further reference in *id.* 70: 1–4.

194. Harrison, J. W. Heslop (1938). "A contribution to our knowledge of the Lepidoptera of the islands of Coll, Canna, Sanday, Rhum, Eigg, Soay and Pabbay (Inner Hebrides), and of Barra, Mingulay and Berneray (Outer Hebrides)." Proc. Univ. Durham Phil. Soc. 11: 10–23.

Lists of many species with a few general habitat notes.

195. Dowdeswell, W. H. & Ford, E. B. (1938). "The Lepidoptera of Cara Island." Entomologist, 71: 82–3.

Nine additional species to the previously recorded 45. Ten butterflies and 44 moths.

196. Balfour-Browne, F. (1938). "The aquatic Coleoptera of the Outer Hebrides. Second paper." Scot. Nat.: 33–46.

Beetles collected on the island of Barra in June and August increase the total number of aquatic species for the island to 42, and the list for the Outer Hebrides generally to 63. There are some habitat notes and a complete list of species.

197. Walker, J. J. (1938). "On the Coleoptera, etc., of the Faroe Islands." Ent. Mon. Mag. 74: 77–82

156 species of Coleoptera as compared with 232 recorded from the Shetlands and 141 from Iceland.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

198. Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1938). "The handbook of British Birds. Vol. 1 (Crows to fly-catchers)." H. F. and G. Witherby, Ltd., 326 High Holborn, London. Price £1. 1*s*. per vol. for subscribers to all five volumes; £1. 5*s*. for single volumes.

A partly rewritten edition containing much new matter, especially on the ecological side, illustrated with small coloured plates of every species in various states of plumage. Indispensable for all field ecologists dealing with birds.

199. Longfield, C. (1937). "The dragonflies of the British Isles." 220 pp. and 260 illustrations. F. Warne and Co., Ltd., Bedford Court, Bedford Street, London, W.C. 2 and 381 Fourth Avenue, New York, U.S.A. Price 7*s*. 6*d*.

Concise reference book for the group, with keys for identifying fresh specimens in the field (but not entirely adequate for preserved ones). Includes useful summary also of many ecological characteristics. (Reviewed in J. Anim. Ecol. (1938) 7: 162.)

200. Lal, K. B. (1938). "On the immature stages of some Scottish and other Psyllidae." Proc. Roy. Soc. Edinburgh, 57: 305–31.

An important new guide to the immature stages of 13 species of jumping plant-lice. Most of the species described are on trees and shrubs: alder, ash, box, hawthorn, *Pyrus* spp., sallow, buckthorn, *Eucalyptus*; a few also on herbs: nettle, willow-herb.

201. Richards, O. W. (1938). "A species of *Sphaerocera* (Diptera, Sphaeroceridae) new to Britain." Proc. R. Ent. Soc. Lond. B, 7:127–30.

Includes a key and notes on *S. micropyga*, *S. crenata*, *S. paracrenata* and *S. falcozi*, of which the third has not hitherto been recorded from England. All have hitherto been rare in collections, probably because they are inhabitants of the nests of birds and mammals situated in very damp places.

202. Edwards, F. W. (1938). "British short-palped craneflies. Taxonomy of adults." Trans. Soc. Brit. Ent. 5: 1–168.

Keys, descriptions and distribution of the 214 British species. Used in conjunction with H. Audcent's paper on the larger species (1932, Trans. Ent. Soc. S. Engl. 8: 1–34), should make it possible to identify any British "daddy-longleg."

203. Edwards, F. W. (1938). "On the British Lestremiinae, with notes on exotic species. 1. [2, 3]. (Diptera, Cecidomyiidae.)" Proc. R. Ent. Soc. Lond. B, 7: 18–24, 25–32, 102–8.

This subfamily has hitherto remained one of the least known groups of British Diptera, no doubt because the species are small and inconspicuous, while few or none of them are of economic importance and (in contrast to the Cecidomyiinae) none of them is a gall-maker. The British material examined consisted largely of adult specimens captured either on windows or in woods and about old logs. Keys and figures are given.

204. Emden, F. van (1938). "On the taxonomy of Rhynchophora larvae." Trans. R. Ent. Soc. Lond. 87: 1–37.

An important paper giving keys to genera and many species of weevils, with considerations of their affinities.

205. Kerrich, G. J. (1938). "A revision of the British species of the genus *Hygrocryptus* Thoms. (Hym., Ichneumonidae, Cryptini)." Trans. Soc. Brit. Ent. 5: 169–77.

Includes key to the six British species.

206. Benson, R. B. (1938). "A revision of the British sawflies of the genus *Empria* Lepeletier (Hymenoptera, Symphyta)." Trans. Soc. Brit. Ent. 5: 181–98.

Includes keys and distribution of the thirteen British species.

207. Sherborn, C. D. & Tams, W. H. T. (1938). "Generic, trivial and specific names." J. Soc. Bibl. Nat. Hist. 1: 130.

General ignorance prevails as to the meaning of these three terms. In *Felis leo*, *Felis* is the generic name, *leo* the trivial name, and *Felis leo* the specific name.

208. Jobling, B. (1938). "The cardboard cell method for the mounting of insects and their parts." Proc. R. Ent. Soc. Lond. A, 13: 55–7.

The cell method is generally used for mounting large specimens, when it is necessary to obtain a permanent microscopic preparation without any distortion of the form by pressure of the cover-glass. The technique which is described here differs from others in the use of cardboard rings instead of those made of glass or metal.

209. Drabble, H. (1937). "Plant ecology." 142 pp. and 12 plates. Edward Arnold and Co., Ltd., 41 Maddox Street, London, W. 1. Price 7*s*. 6*d*.

A convenient and concise textbook describing the main British plant associations (with photographs) and with diagrams showing succession, and a short bibliography. The animal ecologist will find this book useful in any attempt he may make to understand the biotic community.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **144, 150, 182, 186, 242, 253, 259, 265, 267, 271**

210. Nelmes, E. (1938). "A survey of the distribution of the wood ant (*Formica rufa*) in England, Wales and Scotland." J. Anim. Ecol. 7: 74–104.

A comprehensive enquiry aimed at mapping all known records of wood ants in Great Britain. Maps for England and Wales, and for Scotland are shown separately, and the former is overlaid on a map giving general soil character, as judged from the distribution of geological zones and glacial drift. Allowance being made for the different areas covered by various soil types (determined by planimeter), frequencies of ant records are worked out, and show a very marked relation between wood ants and sandy or non-calcareous soils. They also tend to come on well-drained places. The Bagshot sands in southern England are one example of high density of colonies on non-calcareous sand. Chalk and limestone have few colonies. This monograph is valuable, not only in giving these correlations, and a full list of detailed localities and references to all published records, but also in providing a rough guide to the distribution and areal importance of different soil formations in England and Wales. Further factors mentioned as influencing wood ant distribution are woodland distribution, tree felling, light intensity, fires, and game preservation. The last factor results both in destruction of nests and in the deliberate introduction of ants to new localities.

211. Thomas, D. C. (1938). "Report on the Hemiptera-Heteroptera taken in the light trap at Rothamsted Experimental Station, during the four years 1933–1936." Proc. R. Ent. Soc. Lond. A, 13: 19–24.

A 300-candle power electric light about 3 ft. 6 in. above the ground was in continuous use. The trap was fitted with a series of eight killing-bottles, changed automatically at intervals during the night so as to provide evidence of the time of flight of particular species. Capsidae were by far the most abundant Heteroptera to come to light both in numbers of species and of individuals (95% out of a total of 1486). This period from the end of June to the middle of September gave the greatest numbers, but does not correspond very well with the observed occurrence of these species in the field and may possibly be accounted for by diminished activity of male Capsidae after copulation. The Corixidae, Nabidae and Lygaeidae taken were mostly females, the Capsidae mostly males.

212. Edwards, F. W. (1938). "Notes on the Mycetophilidae (Dipt.) obtained by Dr C. B. Williams in a light-trap at Harpenden, Herts." J. Soc. Brit. Ent. (1): 199–202.

Exact records were kept of the climatic conditions and also of the period of the night when the insects were caught. Flies of the subfamily Sciarinae predominated, and by far the greater proportion consisted of females. The species most constantly captured was *Sciara brunnipes*, which has a well-marked flight period in the early part of the night, also some slight indication of another flight at dawn.

213. Woodhill, A. R. (1938). "Salinity tolerance and *p*H range of *Culex fatigans*." Nature, Lond., 141: 920.

Generally regarded as a fresh-water mosquito, this species was bred in the laboratory in sea water of various dilutions. Larvae would not develop normally in a salinity greater than 10 g. per mille. Pupae appeared extremely resistant when transferred from low to high salinity. *p*H within the limits of 4·2 and 9 had no effect on development.

214. Fraenkel, G. & Pringle, J. W. S. (1938). "Halteres of flies as gyroscopic organs of equilibrium." Nature, Lond., 141: 919–20.

The anatomical arrangement of the sense organs at the base of the halteres is such as to resist the forces set up by the vibration of these organs. Experimental evidence further supports the balancer theory and lends no support to the idea that the halteres have a purely stimulatory function.

215. Watson, G. I. (1938). "The jump of fleas." Nature, Lond., 141: 923.

A flea after jumping off turns and travels tail-first through the air, thus placing the heavy end foremost. On landing, the flea faces the direction from which it has come. "If the landing place proved uncongenial, I suppose nothing could get away more quickly than a flea, already facing as it is the way it wishes to return."

216. Mellanby, K. (1938). "Activity and insect survival." Nature, Lond., 141: 554.

Female bed-bugs (*Cimex lectularius*) survived on an average 134 days of starvation when not disturbed, but died if forced to run about for 7 days of starvation. Differences in technique thus probably account for previous range of results found by various investigators. "Field conditions" which affect activity will influence longevity of bed-bugs.

217. Fraser, F. C. (1938). "*Vanessa atalanta* hibernating in Hampshire." Entomologist, 71: 86.

In upper rooms of an old house in December.

218. Warren, B. C. S. (1938). "The flying-habits of butterflies when paired." Entomologist, 71: 114–17.

Confirmation of Donzel's theory that the flying habit is the same in all species of a genus. The female flies in the Satyridae; both sexes fly alternately in four species of Argynnids, in other species the female does; in the "Coppers" the female, in the "Blues" the male flies. In the Pierids the male usually flies, in the Hesperidae it is the female.

219. Rippon, C. (1938). "*Asteroscopus nubeculosa.*" Entomologist, 71: 120.

The emergence or not of any particular pupa of this moth in a particular March is determined the previous autumn.

220. Walsh, G. B. (1938). "Some relations of British Coleoptera to their environment." Trans. Soc. Brit. Ent. 5: 199–222.

Rate of loss of water is greater in dead beetles than in living ones, is proportional to time of exposure, is increased by wind and dependent upon temperature and the size of the elytra. Brachelytra show little resistance to drought conditions and are almost invariably found in a damp environment. Beetles where the elytra are in a fixed position close to the body have only a slow rate of loss of water, e.g. most sandhill species, many weevils and a few water-beetles. It is possible that certain xerophile beetles may possess the power of surviving a certain amount of desiccation better than do other beetles, and of recovering when conditions become damp again.

221. Fisher, R. C. (1938). "Studies of the biology of the death-watch beetle, *Xestobium rufovillosum* De G. II. The habits of the adult with special reference to the factors affecting oviposition." Ann. Appl. Biol. 25: 155–80.

Life of adult, egg laying and hatching. Times of pupation and emergence in the natural habitat, i.e. decayed parts of willow compared with those in buildings. "Indices of suitability" for various combinations of temperature and humidity in relation to egg-laying and hatching are calculated from experimental data.

222. Forestry Commission (1938). "Elm disease. *Ophiostoma ulmi* (Syn. *Ceratostomella* (*Graphium*) *ulmi*)." Leaflet No. 19, pp. 8. (Originally published December 1928; last revised February 1938. Forestry Commission, 9 Savile Row, London, W. 1.)

In this disease, caused by a fungus, the crown of the tree and the ends of the branches wither and lose their leaves, and the tree may die in one to several years, though the proportion killed is small. Two bark beetles (*Scolytus destructor* and *S. multistriatus*) make their breeding galleries under the bark, and those adults emerging before July are probably the most important carriers of the fungus. The disease apparently acts by the fructifications interfering with the flow of moisture through the woody tissues. Since it was first noticed in 1927 the disease has spread over a large area, south of the Scottish Border. A map shows it to be more frequent in the southern half of England (especially in the east) than in the north, in Wales or in Devon and Cornwall.

223. Hendrick, J., Moore, W. & Morison, G. D. (1938). "Activity of the sheep tick." Nature, Lond., 141: 648.

Ixodes ricinus appeared to be active throughout the year in north-east Scotland, seasonal incidence being highest in the summer and lowest in the winter. This finding disagrees with previous observation that activity is confined to spring and autumn periods.

4. PARASITES

See also **174, 185, 190, 215, 216, 223, 259**

224. Thompson, G. B. (1938). "The parasites of British birds and mammals. 18. The mammal-fleas and their hosts." Ent. Mon. Mag. 74: 109–13.

Analysis of the hosts of British mammal-fleas.

225. Thompson, G. B. (1938). "The parasites of British birds and mammals. 19. Further records of *Ornithomyia* spp. from British birds, together with notes." Ent. Mon. Mag. 74: 129–33.

226. Craufurd-Benson, H. J. (1938). "Bionomics of a cattle louse." Nature, Lond., 141: 921.

The apparently high incidence of infestation of dairy shorthorns in Hertfordshire with *Solenopotes capillatus*, and the occurrence of this louse also on cattle in Perthshire and Dumfriesshire, suggests a wider distribution and a greater importance than has hitherto been recognized.

227. Taylor, E. (1938). "Some records of bred Tachinidae (Diptera)." J. Soc. Brit. Ent. 1: 221–3.

Chiefly from Lepidopterous hosts, but some from woodlice.

228. Wilkinson, D. S. (1938). "On the identity of *Apanteles circumscriptus* Nees (Hym., Braconidae)." Proc. R. Ent. Soc. Lond. B, 7: 41–51.

Account of a single species of Hymenopterous parasite, with description, figures, discussion of synonomy, records of distribution and a detailed examination of host records.

229. Edwards, F. W. (1937). "The hosts of *Pterobosca paludis* Macfie." Ent. Mon. Mag. 73: 164.

Enallagma cyathigerum, Coenagrion pulchellum, Ischnura elegans, Libellula quadrimaculata and *Brachytron pratense* (all dragonflies).

230. Musgrave, A. J. & Mackinnon, D. L. (1938). "Infection of *Plodia interpunctella* (Hb.) (Lepidoptera, Phycitidae) with a Schizogregarine, *Mattesia dispora* Naville." Proc. R. Ent. Soc. Lond. A, 13: 89–90.

The parasite is a highly pathogenic Schizogregarine found in the fat-body and haemocoele of the larvae, pupae and adults of this moth. It is possible that the larvae are infected by ingesting the spores in contaminated food.

5. FOOD AND FOOD-HABITS

See also **145, 172, 251, 256, 261**

231. Berry, J. (1938). "The longtailed field mouse (*Apodemus sylvaticus*) as a destroyer of salmon ova." Avon Biol. Res. No. 5, 1936–37: 67–9.

Nest of this species in a hatchery box contained ova, and a mouse was seen to remove from water and eat one.

232. Braid, K. W. (1936). "Poisonous plants with special reference to the poisonous properties of bracken (*Pteridium aquilinum*)." Scot. J. Agric. 19: 247–51.

Species poisonous to stock in Scotland include yew (*Taxus baccata*), water dropwort or water hemlock (*Oenanthe crocata*), ragwort (*Senecio jacobaea*), and bracken. Experiments and observations proved that bracken can poison (often fatally) horses and cattle, but probably does not affect sheep much.

233. Bisset, N. & Rees, J. (1937). "Poisoning by ragwort." Welsh J. Agric. 13: 321–5.

Three small outbreaks killing cattle in South Wales. Although the cinnabar moth is very abundant, there seems little prospect of it controlling ragwort in this region.

234. Currie, P. W. E. (1938). "Notes on the association of thrushes and hawfinches." London Nat. for 1937: 87–8.

Hawfinches eating remains of yew berries rejected after being partly digested by mistle thrushes in a beech-yew wood on the Surrey Downs. The finches were seen to associate with the mistle thrush flocks at this time.

235. Buckstone, A. A. W. (1938). "Fish attacked by dragonfly larva." Entomologist, 71: 128.

Six-inch roach with a large dragonfly larva attached to one of its gills.

236. Dallman, A. A. (1937). "The pollination of *Picris echioides* L." North Western Nat. 12: 403–4.

A list of insects (six flies) visiting flowers.

237. Dallman, A. A. (1937). "Notes on the Hole of Horcum, Saltersgate, North Yorkshire. 5. The pollination of *Cornus suecica* L." North Western Nat. 12: 388–9.

A list of insects (two beetles, seven flies, and one moth) visiting this local plant.

238. Carpenter, G. D. Hale (1938). "*Arctia plantaginis* Linn. (Lep.) eaten by swifts." J. Soc. Brit. Ent. 1: 213–14.

This moth was abundant at the time and was being extensively preyed upon. For other records of the food of birds, see *id., ibid.*: 214 and **R. Cottam**, *ibid.* 235–6.

239. Morley, A. M. (1938). "More ravages of clothes moths." Entomologist, 71: 43–4.

Acompsia pseudospretella larvae feeding on the pupae of *Nyssia lapponaria* and *N. zonaria* in a garage.

240. Buckstone, A. A. W. (1938). "*Pieris rapae* a cannibal." Entomologist, 71: 34.

P. rapae devouring larvae of *P. brassicae.*

241. Hopf, H. S. (1938). "Investigations into the nutrition of the ash-bark beetle, *Hylesinus fraxini* Panz." Ann. Appl. Biol. 25: 390–405.

Food relations based on investigations into the enzymes of the alimentary canal and a comparative analysis of ash bark and frass of the beetle.

242. Freeman, P. (1938). "Notes on the nesting of five species of solitary wasps (Hymenoptera, Sphecoidea)." Proc. R. Ent. Soc. Lond. A, 13: 1–6.

Rhopalium clavipes, Psenulus atratus, Trypoxylon figulus, T. clavicerum and *T. attenuatum* were observed nesting in the straws of a thatched summer-house during the summer of 1936 at Slough, Bucks. When a wasp was seen going into a straw, the end of the straw was pinched between finger and thumb and the straw pulled out. The adult was kept for reference, measurements of the cells and counts of the prey were made, the prey was preserved in 70 % alcohol and eventually identified. The prey of the first two species consisted of Psocoptera and Aphididae respectively and of the last three immature spiders.

6. POPULATIONS

See also **144, 145, 162, 185, 186, 210, 280, 282, 284, 286, 287**

243. Johnston, F. J. (1938). "The grey squirrel in Epping Forest." London Nat. for 1937: 94–9.

This area remained uncolonized until a late date (1935) since when grey squirrels have been destroyed as much as possible. One definite almost fatal attack of a grey upon a red squirrel observed. Other fresh-killed red squirrels were found, though there was no proof that grey squirrels had killed them. There was decrease in red squirrels after the arrival of the grey.

244. Gethin, R. G. (1936). "Pine marten visitor." Irish Nat. J. 6: 145–6.

Pine martens have been preserved at Curraghmore (the Marquess of Waterford's estate) during the last 35 years, and have increased a good deal, but keep chiefly to the woods.

245. Southern, H. N. (1938). "Isle of May breeding census." Scot. Nat.: 1–2.

Summary of investigation described in J. Anim. Ecol. (1938) 7: 144–54. (See **185**.)

246. Bletchly, J. D. (1938). "Some observations on the breeding-habits of birds." Brit. Birds, 32: 8–12.

Data on the incubation and fledging periods (and mortality rates) of birds in a mixed cultivated and woodland area in Gloucestershire, in 1930–33.

247. Wild, S. V. (1937). "A census of singing birds." (1937). North Western Nat. 12: 143–51.

A census of singing yellow buntings in 1935–36 on an area of two to three acres. In the second year the other birds were also included (ten species).

248. Venables, L. S. V. (1938). "Birds seen in two winter transects of the North Atlantic." Brit. Birds, 31: 295–6.

The commonest bird was kittiwake. These appear to be more numerous in winter, when fulmars and great shearwaters decrease.

249. Mitchell, M. (1938). "The rook (*Corvus frugilegus*) population of North-west Denbighshire." J. Anim. Ecol. 7: 20–1.

Nest density on about 113 sq. miles was about 14. Habitat preferences are analysed: no nests occurred above 600 ft.

250. Ward, J. H. (1936). "Rook roosts in the Manchester area." Naturalist: 153–6.

Roosting at various points, from about July to March. Notes on feeding grounds and flight lines.

251. Moeran, D. M. (1937). "Ravens in Co. Donegal." Irish Nat. J. 6: 155–6.

Great abundance of ravens in wild hill country attributed to epidemic among sheep said to be due to blowfly, and consequent large amount of carrion.

252. Duncan, A. B. (1938). "The magpie in Scotland." Scot. Nat.: 65–79.

References cover a period of 90 years, during which time it has steadily decreased. With the present break-up of large estates, magpies will probably tend to increase. Distribution records are given according to counties. The magpie is not found in Orkneys, Shetlands or Hebrides.

253. Longfield, C. (1938). "Observations on a colony of house martins, 1929–1935." London Nat. for 1937: 89–91.

Observations on a colony in a limestone cliff on the coast of County Cork, Eire, with notes on fluctuation in population (between ten and two pairs at limits), habits in nest-building, etc.

254. Nicholson, E. M. (1938). "Publication of the British Trust for Ornithology. The index of heron population, 1937." Brit. Birds, 31: 341–4.

A very large series of sample counts was made, covering about half the total breeding heron population. Comparisons with previous years, partly recalculated on a revised basis, show that extremely little change has taken place in the British Isles as a whole, though local changes are quite large. The result suggests an ability of the population to adjust itself as a whole.

255. Booth, H. B. (1936). "Fulmar petrels nesting on the Farne Islands." Naturalist: 199.

One pair nested, for first time, in 1935. In 1936 there were four birds incubating.

256. Stewart, M. (1938). "Notes on the gannetries of Sule Stack and Sula Sgeir." Brit. Birds, 31: 282–94.

There is a brief account of these two small islets, which lie north and north-west of Scotland (east and west of North Rona), and a history of work on their gannet populations. In spite of certain technical difficulties a rough estimate was made of the numbers: in 1937, about 3500 breeding pairs on Sule Stack and about 4500 on Sula Sgeir. There has been decrease on the latter, attributed to removal for food of large numbers of nestlings by men from Ness, in the Isle of Lewis. There is at present no legal means of preventing this destruction after 1 August.

257. Slack, H. D. (1937). "Notes on the viability of *Bacillus salmonicida* Emmerich and Weibel." Ann. Appl. Biol. 24: 665–72.

258. Cowley, J. (1938). "Quantitative methods of local entomofaunistic survey." Entomologist, 71: 8–12.

Notes on Valle's scheme for quantitative survey work as well as the marking methods of Borror, Swynnerton and Fletcher. Jackson's formula for estimating the total population from the recovery index and Balfour-Browne's estimation of the relative degree of concentration of a species in its different habitats are also mentioned.

259. Morison, G. D. (1937). "Some results of trapping the sheep blowfly (*Lucilia sericata* Meigen)." Scot. J. Agric. 20: 123–34.

This is the chief species responsible for "striking" sheep in Great Britain. A standard baited trap was used to study population distribution and numbers. 152,815 flies were trapped at different stations near Aberdeen in 1933–34, for periods varying from 39 to 165 days. Of these 6039 were *L. sericata*. The results are discussed in relation to habitat and weather, but the conclusions are not easily summarized. Notes are given also on other species of flies, on baits, and there is a useful bibliography, much of which concerns the blowfly problem in Australia.

260. Jones, D. P. (1936). "Gall midges affecting grass seed production in mid-Wales." Welsh J. Agric. 12: 192–7.

Five grasses of importance in Wales are affected by gall-flies, of which the species and their host-plants are discussed. The loss to the seed crop of grass is sometimes considerable.

261. Fenton, E. Wyllie (1937). "Biological notes for 1936." Scot. J. Agric. 20: 63–7.

Among other topics records serious damage to heather on certain moors in the west of Scotland, through heather beetle (*Lochmaea suturalis*), possibly also due to a fungus disease. There is also a discussion of the ecology of bracken, and the relation of its spread to reduction of cattle grazing. The house sparrow is pilloried as a pest.

262. Braid, K. W. & Tervet, I. W. (1937). "Certain botanical aspects of the dying-out of heather (*Calluna vulgaris* Hull.)." Scot. J. Agric. 20: 365–72.

In a discussion of the increase of bracken at the expense of heather on Scottish hills, it is suggested that although heather beetle and frosts are responsible for much heather destruction, there are also other factors such as fungus disease to be taken into account. A scale insect (*Lepidosaphis ulmi*) may also damage tissue. The ecology and distribution of certain fungi on heather are described.

263. Beak, T. W. (1938). "Investigation of the fauna of a water meadow carrier." Avon Biol. Res. No. 5, 1936–37: 29–41.

Bottom collections with a grab in a stream for seven months, provided figures for quantitative estimation of fauna in four different types of bottom. Seasonal variations are noted.

264. Beak, T. W. (1938). "Methods of making and sorting collections for an ecological study of a stream." Avon Biol. Res. No. 5, 1936–37: 42–6.

Discusses methods of taking bottom samples; also a new way of sorting samples, being an adaptation of Liddle's apparatus for sorting out animals from soil by means of high density liquids.

265. Stephen, A. C. (1938). "Production of large broods in certain marine Lamellibranchs with a possible relation to weather conditions." J. Anim. Ecol. 7: 130–43.

Sample counts of populations of two molluscs, *Tellina tenuis* and *T. fabula*, in the intertidal zone in the Clyde Basin were done from 1926 to 1937, and a marked fluctuation in the abundance of young was found, with peaks every three or four years: 1926, 1930, 1933, 1936 and 1926, 1930, 1933, 1935, respectively. This fluctuation is compared with meteorological factors (sun, rain and temperature) and a provisional correlation made between high "spat" years and high temperature. Tables of the size distribution of the two species in the samples in each year are given.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **162, 183, 211, 212, 217, 218, 255, 280, 281**

266. Leach, E. P. (1938). "Recovery of marked birds." Brit. Birds, 31: 302–8, 322–9.

267. Southern, H. N. (1938). "The spring migration of the swallow over Europe." Brit. Birds, 32: 4–7.

The average arrival dates of swallows in Europe are mapped with reference to movements of the 48° F. isotherm for the same period. A provisional correlation is made.

268. Thomson, A. Landsborough (1938). "A Publication of the British Trust for Ornithology. Report of the Bird-ringing Committee: progress for 1937." Brit. Birds, 31: 345–51.

The bird-ringing scheme, carried out since 1909 under the auspices of "British Birds", has passed to the control of the Trust, with headquarters for this section of its research, at the British Museum (Natural History). In 1937, 21,900 birds were trapped and ringed, and 23,281 nestlings: total, 45,181 birds. Details are given of numbers ringed by different observers, the numbers of each species ringed in 1909–36, and in 1937, and the percentage recovered of those ringed in 1909–36.

269. Lack, D. & Lockley, R. M. (1938). "Skokholm Bird Observatory homing experiments. 1. 1936–37. Puffins, storm-petrels and Manx shearwaters." Brit. Birds, 31: 242–8.

Some preliminary results of ringing birds of which the results are difficult to summarize. The authors state that "at this stage the experimental data do not warrant further discussion". One Manx shearwater taken to Venice (930 miles away) and released on 10 July 1937 was recovered on Skokholm (S.W. Wales) on 24 July 1937. If the bird came back by sea it must have gone at least 3700 miles. Venice is outside the known range of the species. Other birds released in Ireland, Scotland, Faeroes, and places inland in England, were also recovered. The number of shearwaters originally ringed is not stated. There is a short but useful list of references to foreign investigations on homing.

270. Moreau, R. E. (1937). "Migrant birds in Tanganyika Territory." Tanganyika Notes & Records, No. 4.

Contains, as well as a survey of tropical migration, a valuable section on Palaearctic migrants in their winter quarters with a summary of what is so far known of distribution, habitat selection in comparison with summer quarters, condition of gonads prior to spring migration, incidence of moults and records of singing.

271. Temperley, G. W. (1938). "Ornithological report for Northumberland and Durham for the year, 1937." Vasculum, 24: 55–9.

Discusses the weather and its effect on bird movements. Gives distributional, abundance, nesting and other notes.

272. Dannreuther, T. (1938). "Migration records, 1937." Entomologist, 71: 60–6.

A general summary for the year.

273. Garrett, F. C. (1938). "Migrant Lepidoptera in 1937." Vasculum, 24: 19–20.

Some northern records.

274. Grant, Mrs K. (1938). "A migration of cabbage white butterflies in Hertfordshire in May, 1937." Entomologist, 71: 103–7.

275. Maldwyn Davies, W. & Whitehead, T. (1938). "Studies on aphides infesting the potato crop. VI. Aphis infestation of isolated plants." Ann. Appl. Biol. 25: 122–42.

Winged aphides had no difficulty in detecting and colonizing isolated plants which can be reached from a distance of at least a quarter of a mile.

276. Stephen, A. C. (1938). "Temperature and the incidence of certain species in Western European waters in 1932–34." J. Anim. Ecol. 7: 125–9.

Accompanying the unusually high temperatures in the Atlantic in 1932–34, a good many animals from more southern waters were found in abnormal frequency round the British Isles. These animals include whales and dolphins, fish, tunicates, pelagic molluscs and cirripedes, siphonophores and Protozoa. Attention is also drawn to certain other phenomena, including the disease in eel-grass (*Zostera*), unusually great appearance of the young of certain fish and molluscs, and unusual local abundance of certain British species.

277. Storrow, B. (1938). "Faunistic and hydrographic changes." Nature, Lond., 141: 798–9.

The recent occurrence of seven species of fish and one species of crab not usually found on the Northumberland coast is explained by the established abnormal activity of Atlantic water around the north of Scotland, followed by a southern movement of colder Norwegian water driving the animals south into the North Sea.

278. Stelfox, A. W. (1936). "*Physalia*, 'the Portuguese man-of-war', and *Velella* in Irish waters." Irish Nat. J. 6: 142–3.

Velella sp. seen in Bantry Bay in July 1935. This siphonophore is not infrequent in some years; but *Physalia* is very rare and has not been definitely recorded for a hundred years, although in exceptional years it is seen off the south-west coast of England.

279. Forrest, J. E. (1938). "*Velella spirans* (Forskal) in the Outer Hebrides." Scot. Nat.: 10.

This siphonophore appeared in fair abundance off the island of Barra in July 1937.

8. REPORTS OF ORGANIZATIONS

280. British Trust for Ornithology (1938). Fourth Report, Summer 1938. 33 pp.

Arrangements have now been made to set up the Edward Grey Institute of Field Ornithology in Oxford, to provide better facilities for bureau work and a research centre. The "British Birds" bird-ringing scheme has been transferred into the control of the Trust, with headquarters in the British Museum (Natural History). Investigations include the little owl enquiry (whose report was reviewed in J. Anim. Ecol. (1938) 7: 161–2); woodcock distribution and ecology; woodland bird distribution; song periods; lapwing habitats; sample heronry census covering a large part of the country, certain habitat and distribution enquiries through local natural history societies (magpie, coot and red-backed shrike). New enquiries being started include survey of black-headed gull breeding colonies; corncrake distribution; bridled guillemot varieties. Local bird census work round Oxford was continued. The work of this organization is expanding steadily, as is the support given to it by ornithologists.

281. Skokholm Bird Observatory (1937). Report for 1937. 22 pp.

The Observatory was started in 1936, and is run by R. M. Lockley in co-operation with various observers and organizations. In 1937 there were over a hundred observers, not counting day visitors; 4404 birds were ringed (2059 as adults), also 1797 Manx shearwaters in a special investigation on homing. The figures for census of breeding birds over ten years are given. The neighbouring island of Grassholm has, through the action of its proprietor, been placed partly under control of the Observatory for bird watching, and activities such as gannet ringing. A number of migration notes, etc., are included, also parasite records, and information about grey seals, Soay sheep, and rabbits. In 1936 and 1937 a virus disease, myxomatosis, was introduced with the aim of controlling rabbit numbers. The numbers in 1936 were estimated at about 20–25 per acre. Although the disease spread to a certain extent, it did not appreciably decrease the population, and it is thought the virus has died out. There is a large population also of house mice (*Mus musculus*) introduced thirty years ago, living all the year round out of doors. There are a few notes on butterfly migrants and on plants, in particular bracken, which is said to favour increase in gulls by providing nesting cover. The effect of bracken on various birds is summarized.

282. Bureau of Animal Population, University of Oxford (1937). Annual Report, 1936–37. 38 pp.

Reviews general position of population research in relation to human affairs; and the particular researches of the Bureau on vole populations (*Microtus agrestis*), game birds and animals, certain North American species (including the snowshoe rabbit, *Lepus americanus*, and the arctic fox *Alopex lagopus*), and special surveys including semi-wild animals at Whipsnade, squirrels on a Hampshire estate, habitats of mice and bank voles, moles; also introduced animals, including grey squirrels. Attention is specially given in these researches to the structure and fluctuations of the populations.

283. Lancashire and Cheshire Fauna Committee (1937). Twenty-third Annual Report and Report of the Recorders for 1936. 52 pp.

A valuable list of local records often with habitat notes, covering vertebrates, various insect groups, *Arachnida*, woodlice, non-marine Mollusca and plant-galls. The report gathers together a large amount of scattered information from many observers. There are also some ecological notes on selected species of birds: grey wagtail, lesser redpoll, and little owl. Notes include habitats at different seasons, nesting sites, and numbers.

284. Yorkshire Fishery District, Board of Conservators (1937). Seventy-first Annual Report on the salmon, trout and freshwater fisheries in Yorkshire. (By **W. T. Clarke.**) 47 pp.

Contains figures of the number and weight of salmon and migratory trout caught in river, estuary and sea (total 2425 salmon, weighing 35,198 lb.; 1788 migratory trout, weighing 6669 lb.), notes on coarse fish, fish passes to counteract the effect of dams and weirs, pollution (which is decreasing), and the recovery of marked salmon and trout.

285. West Riding of Yorkshire Rivers Board (1937). Forty-second Report, 1934–37. Wakefield, Yorkshire.

This report, though dealing mostly with administrative measures, gives a good idea of the intricate relations between the various interests using rivers: water-supply, sewage, industrial effluents, land drainage, fisheries, etc. The main subject dealt with is sewage and effluent disposal, but it is pointed out that pollution is now less an obstacle to salmon entering the Yorkshire rivers (which they still do in some numbers), than the large amount of yellow alluvial silt in suspension in tidal waters, and the construction of impassable weirs and dams. The Board claims that pollution is now being dealt with more and more effectively at the sources. The clean rivers, Ure, Nidd, Wharfe, Aire (part), Ouse and Ribble (West Riding reaches) "have all remained in good condition and are well-stocked with fish". Chemical and water-flow data for some rivers are given.

286. Avon Biological Research (1938). Annual Report, No. 5, 1936–37. 80 pp. (University College, Southampton. Price 2*s*. 6*d*.)

The research deals mainly with salmon and trout in the River Avon, but takes a wide view of the environment and of other species of animals. Some separate papers in the Report are noticed elsewhere.

287. Freshwater Biological Association of the British Empire (1938). Sixth Annual Report, for the year ending March 31st, 1938. 73 pp.

The work of this organization, with laboratory at Windermere, is mainly pure research with a bearing upon economic problems such as freshwater fisheries and water supply. The investigations around Windermere embrace a wide scope, including the physical conditions and vegetation, and also surveys of animal ecology, among which are: the relation of lake bottom deposits and physiographical history of Windermere to the flora and fauna; the distribution of invertebrate animals in the Lake District (mainly with reference to Mollusca and insects); and population studies of salmon, etc. The Association appears to be extending its membership widely among biologists, fishery organizations and water-supply undertakings.

288. Marine Biological Station at Port Erin, Isle of Man (1937). Report for 1937 (No. 50). 24 pp.

Includes notes on oyster culture experiments, and a list of corrections and additions to Moore's "Marine Fauna of the Isle of Man" (see Notice No. **143**).

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